

# The American Midland Naturalist

Devoted to Natural History, Primarily  
that of the Prairie States

Founded by J. A. Nieuwland, C.S.C. †

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# The American Midland Naturalist

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## Studies on *Ambrosia*, I.

### The inheritance of floral types in the ragweed, *Ambrosia elatior* L.<sup>1</sup>

K. L. Jones

#### Introduction

There is disagreement over the status of the species *Ambrosia elatior* L. and *A. artemisiifolia* L. This is partly because of their treatment in the more commonly used manuals: Gray's Manual, for example, mentions only the latter, whereas, in Britton and Brown, *Ambrosia elatior* L. is described and *A. artemisiifolia* L. is given as a synonym. The writer has minutely examined some 30,000 individuals of the lesser ragweed, grown in his cultures the past six years at the University of Michigan Botanical Gardens. The characteristics which have been used to establish these species (Linnaeus, 1753; Rydberg, 1922) are largely quantitative, and in culture, are too variable to justify any segregation. Rydberg (1922) for example, restricts *A. artemisiifolia* L. to the Atlantic seaboard and makes *A. elatior* L. the ubiquitous species. The contrasting characteristics stated by this author are:

*Ambrosia elatior* L.: Stem 3-10 dm. high; leaves bipinnatifid or the upper less divided; staminate involucre 3 mm. wide; body of fruit 3 mm. long.

*Ambrosia artemisiifolia* L.: Stem 5-10 dm. high; leaves pinnatifid or the upper simple; staminate involucre fully 4 mm. wide; body of fruit 2.5-3 mm. long.

The plants which the present author grew from seed obtained locally at Ann Arbor, Michigan, and which would be *A. elatior* L. according to Rydberg, were characterized as follows: Stem 0.5-19.5 dm high; leaves usually bipinnatifid but ranging from entire to tripinnatifid; staminate involucre 2-20 mm wide; body of fruit 1.5-5 mm. long. The offspring of one plant may exceed the total range of variability in all those characteristics which have been used to discriminate between the two species. Consequently, the writer believes that the name *Ambrosia elatior* L. had better be retained since it has priority of position in the Species Plantarum.

The occurrence of aberrant floral types in *A. elatior* L. has long been known to field botanists, and this information has filtered into most manuals. Three floral types occur: (1) Normal type (Figs. 1 and 2); monoecious; pistillate heads borne laterally in leaf axils, staminate heads in terminal racemes. (2) Intermediate type (Figs. 3 and 4); monoecious; pistillate heads

<sup>1</sup> Papers from the Department of Botany, University of Michigan, number 510.

borne laterally and also in racemes where they accompany staminate or androgynous heads. (3) Pistillate type (Figs. 5 and 6); plant entirely pistillate: pistillate heads borne laterally and in racemes. There are no staminate individuals. All plants bear pistillate heads laterally and hence the types differ only in their terminal inflorescences.

The following description of the floral types is based upon a study of *A. elatior* L. growing wild in the vicinity of Ann Arbor, Michigan, where there is a remarkable array of interesting forms; from my cultures, which were mostly of local origin, but also contained plants from Florida, North Carolina and Arkansas; from herbarium specimens in the University of Michigan Herbarium, and the Swan-Myers Herbarium, the latter furnished through the kindness of O. C. Durham.

#### I. NORMAL TYPE. (Monoecious form 1 and 2).

Locally, at Ann Arbor, over 95% of *A. elatior* L. plants are of the normal type. (Figs. 1 and 2). From the information I have been able to obtain, this type is always predominant throughout the range of the species. In the normal type the distribution of the flowers is roughly like that of *Zea Mays*. The staminate flowers are borne in terminal inflorescences and the pistillate flowers are produced laterally. The minute flowers are in heads; the terminal inflorescence is really a raceme of heads. A staminate head consists of 20-30 flowers, partially concealed within a nodding, saucer-shaped involucre of united bracts which is about 3 mm. wide, and is attached to the rachis by a stalk less than 3 mm. long. At times the staminate racemes are compound. A staminate flower (Fig. 7) has a perianth of one whorl, which is funnelliform, and five toothed; the five anthers are distinct and surround a vestigial pistil which is uniformly cylindrical except for a dilated tip.

Pistillate heads (Fig. 8) are in small groups, sessile and erect in the axils of leaves, bracts or at the base of staminate racemes. The involucre of united bracts fits tightly against the single pistil which it harbors, except for the long, forked style which extends through its subulate beak. There are never stamens nor rudiments of any parts of a staminate flower within a normal pistillate head of this type. The body of the involucre fruit is obovoid, about 3 mm. long, with a series of 4-10 short spines. The pericarp is black and rigid, and contains one relatively large seed in which the food is stored in cotyledons.

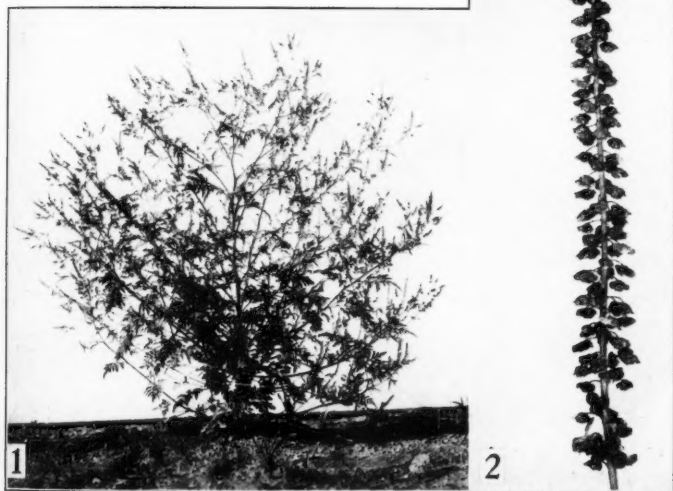
#### II. INTERMEDIATE TYPE. (Monoecious form 3).

The intermediate type (Figs. 3 and 4) differs from the normal type in that the pistils, in addition to being produced laterally, occur also in the terminal racemes along with staminate flowers. In the distribution of pistils in the terminal inflorescences, this type has been observed to range from individuals which would be pistillate but for one staminate flower in one androgynous head, to individuals which would be normal but for one pistil in one androgynous head. It is even possible that intermediates border still nearer the normal and pistillate types, because, in prepared slides a pistil has been

found to harbor a functional anther in its style (Fig. 9) and a staminate flower was sectioned in which a free ovule was present in place of a stamen (Fig. 10.) These examples are similar to the interesting findings of Yampolsky (1934) on *Mercurialis*. A list of intermediate types could be given which would almost satisfy all the possible numerical combinations and positions of stamens and pistils, in individuals bearing scores of racemes each of which

Fig. 1. Normal type; monoecious form 1 or 2.

Fig. 2. Normal type; monoecious form 1 or 2; raceme of staminate heads.



might contain 150 heads with an average of 20 flowers per head. The following list of types, therefore, while tedious, is but a skeleton classification.

1. Plants entirely pistillate but for one androgynous head.

Such androgynous heads, which yield functional pollen and seed, are not confined to plants that are predominantly pistillate. The involucre may be staminate, pistillate, or

a bizarre combination of these two. The head consists of staminate flowers and generally free, i.e. non-involucrate pistils. If the involucre is pistillate or nearly so, the ovary will be at least partially inclosed. The actual and relative number of staminate flowers and pistils within a head is variable. The following record of dissections describes a few representative types of androgynous heads:

- a. Involucre staminate; seven normal staminate flowers, one pistil.
- b. Involucre staminate; seven staminate flowers, two of which were contabescent and growing out of an ovary which set seed.
- c. Involucre staminate; one staminate flower, one pistil. Staminate flower produced functional pollen and grew from an aborted ovary.
- d. Involucre sectorially staminate and pistillate; one pistil with style through beak but the other half of the involucre saucer-shaped holding two staminate flowers.
- e. Involucre pistillate; two pistils with their styles extending through beak. Nine staminate flowers entirely concealed within involucre.

A confusing factor in the study of the intermediate type is the occasional lack of correlation between the form of the involucre and the floral structures contained therein. (see par. "e" above.) An involucre of staminate type may contain one to three functional pistils and no staminate structures. An involucre of the pistillate type, fully developed with spines and beak, may completely incase a dozen staminate flowers and bear no pistil; here, the pollen may never escape even though the anthers dehiscence normally.

2. Plants entirely pistillate but for one staminate head. This staminate head is usually terminal, although perhaps only because in such a position it is least likely to be overlooked.

3. Plants predominantly pistillate; a few staminate heads.

4. Plants having approximately the same number of staminate and pistillate heads and the two irregularly distributed.

5. Plants having approximately the same number of staminate and pistillate heads and the two occurring in segments of the racemes in serial alternation.

6. Plants with predominantly staminate racemes; a few pistillate heads present.

7. Plants with staminate racemes but for one pistillate or androgynous head.

### III. PISTILLATE TYPE. (Figs. 5 and 6).

Plants of this type bear only pistillate heads laterally in the leaf axils and terminally in long racemes. In adverse environments one may find plants which are pistillate because they are so stunted that no racemes develop. These individuals may be potentially normal, intermediate or pistillate.

#### Methods

The writer began his studies of the sex condition in *Ambrosia elatior* L. during the summer of 1929. Previous to this the only work on the problem was an experiment by Garner and Allard (1920) in their well known investigations on photoperiodicity. Plants growing in the environs of Ann Arbor were examined and these data contributed to the classification of the floral types just described. The distribution in nature suggested that the genetic factors were "differential" (Sharp, 1924) and the environmental factors "conditional" in the development of the unlike types. Often normal, intermediate

and pistillate plants were in such close proximity that their roots were intermingling. Wherever the species occurred in any profusion the three sex types were present and the normal type predominated.

The initial collection of seed was necessarily from wild plants. The achenes are too numerous to be collected in the field; Stevens (1932) reported 3,380 on a representative plant. Collecting was done by removing entire

Fig. 3. Intermediate type; monoecious form 3.

Fig. 4. Intermediate type; monoecious form 3;  
raceme of pistillate and staminate heads.



plants and storing them individually in large paper bags. After a specimen had dried it was crushed in the bag and winnowed over an electric fan to secure the seed free from leaf fragments.

Neither freshly harvested nor old seed will germinate without special treatment. Davis (1930) reported that *Ambrosia trifida* seed germinate if

after-ripened at 5 degrees C. one to two months. This method was satisfactory for *A. elatior*. The seed must be kept moist while after-ripening or there will be no germination. Sowings were made in sterilized soil. Germination was highest at 35 degrees C. Each seedling was transferred to a separate pot and labelled. If plants were later grown in the field the label accompanied the plant. The importance of thus avoiding contamination in growing a common weed is obvious.

Controlled pollination is impossible in the field because the plants are wind-pollinated, ubiquitous and the flowers are minute and inconveniently distributed. Seed will not set if the entire plant is bagged with cellophane. Consequently plants must be grown out of season in the greenhouse. Unfortunately *A. elatior* does not thrive under these conditions. The plants require strong light, a long photoperiod and a high temperature. They are very susceptible to white fly and thrips. If grown in the winter most individuals will produce few or no racemes and one is fortunate to secure a dozen viable seed from a plant.

Sowings in early March gave the best results. For example, cultures planted March 10th flowered from April 30th to July 31st. Pollination of ragweeds in nature, in Ann Arbor, begins the third week in August. In making crosses the plants used as female parents were kept emasculated, which requires daily examination, and placed in contingent rows with pollen parents of a given type. Contamination was obviated by maintaining but one type as a pollen parent a season or by utilizing the greenhouses at the Botanical Gardens and at the University of Michigan campus, the two being over a mile apart.

### Results

#### a. THE GENETICAL BEHAVIOR OF PISTILLATE PLANTS.

##### *F*<sub>1</sub> open-pollinated.

The progeny of wild, open-pollinated pistillate plants were cultured in the field. All the seed produced by a plant were sown; each culture was derived from a single plant. The results are given in Table 1.

TABLE 1  
*F*<sub>1</sub> progeny of open-pollinated, pistillate plants.

Culture	No. Plants	No. N	No. I	No. P	% N	% I	% P
23P	531	29	115	387	5.4	21.6	72.8
96P	97	21	51	25	21.6	52.5	25.7
40P	806	239	360	207	29.6	44.6	25.6
33P	325	92	123	110	28.3	37.8	33.8
150P	642	218	184	240	33.9	28.6	37.3
Total	2401	599	833	969	24.9	34.6	40.3

N; normal type, monoecious form 1 or 2.

I; intermediate type, monoecious form 3.

P; pistillate type.

Each of the cultures was derived from one seed parent; e.g. 23P was produced by pistillate plant number 23.

An examination of Table 1 shows that in every instance the offspring of pistillate plants consisted of normal, intermediate and pistillate individuals. The frequency of each type was extremely variable but the normal type was never predominant.

In addition to the foregoing, seventeen cultures (2,690 plants) of similar origin were grown from which the writer secured incomplete data because he was not yet inured to certain inconveniences concomitant with a study of ragweed by one sensitized to its pollen. All of these cultures contained the three sex types; normal plants comprised from 6-30% of each culture.



Fig. 5. Pistillate type.

Fig. 6. Pistillate type; raceme of pistillate heads.

$F_2$  open-pollinated.

Pistillate plants were selected from the  $F_1$  cultures 23P and 81P because they had given the highest percentage of the pistillate type. Culture 81P was among those from which data were incomplete; it consisted of over 50% pistillate plants. The  $F_2$  cultures derived from these are presented in Table 2.

%P  
72.8  
25.7  
25.6  
33.8  
37.3  
—  
40.3

ed by



TABLE 2

F<sub>2</sub> progeny of open-pollinated, pistillate plants.

Culture	% Germ	No. plants	No. N	No. I	No. P	% N	% I	% P
23P-1P	84.4	201	21	112	68	10.4	55.7	33.8
-2P	43.2	104	47	53	4	45.1	50.9	3.8
-4P	50.8	112	32	54	26	28.5	48.2	23.2
-5P	59.2	137	11	43	83	8.0	31.3	60.5
-6P	76.8	142	22	80	40	15.4	56.3	28.1
-8P	69.2	82	3	32	47	3.6	39.0	57.3
-10P	47.2	104	32	40	32	30.7	38.4	30.7
-11P	75.2	165	14	97	54	8.4	58.7	32.7
-12P	62.8	148	22	74	52	14.8	50.0	35.1
-13P	48.4	109	4	46	59	3.6	42.2	54.1
-14P	55.2	139	7	68	64	5.0	48.9	46.0
-23P	19.6	49	2	26	21	4.0	53.0	42.8
-26P	80.4	170	3	69	98	1.7	40.5	57.6
-28P	71.2	107	7	26	74	6.5	24.2	69.1
-32P	87.2	183	36	58	89	19.6	31.6	48.6
-33P	70.8	166	22	72	72	13.2	43.3	43.3
-35P	82.4	198	115	79	4	58.0	39.8	2.0
-36P	84.4	193	60	83	50	31.0	43.0	25.9
-37P	84.4	199	13	46	140	6.5	23.1	70.3
-38P	68.4	166	45	63	58	27.1	37.9	34.9
-39P	72.8	172	7	47	118	4.0	27.3	68.6
Total	66.3	3046	525	1268	1253	17.2	41.6	41.1
81P-4P	58.4	122	12	49	61	9.8	40.1	50.0
-6P	91.6	219	26	95	97	11.9	43.5	44.4
-8P	63.2	154	24	62	68	15.5	40.2	44.1
Total	71.0	494	62	206	226	12.5	41.7	45.7
All	67.0	3540	587	1474	1479	16.5	41.6	41.7

The F<sub>2</sub> results were comparable in many respects to the F<sub>1</sub>. Three sex types appeared in each F<sub>2</sub> culture. The normal type was predominant in only one culture, 23P-35P. The frequency of each sex type was extremely variable with the following ranges: normal, 1.7%-58.0%, intermediate, 23.1%-58.7%; pistillate, 2.0%-70.3%. None of the cultures had as high a percentage of pistillate plants as the F<sub>1</sub> parent culture; however six cultures had a lower percentage of the normal type. The percentage of intermediate plants was higher in every F<sub>2</sub> culture.

### F<sub>3</sub> open-pollinated.

Pistillate plants were selected from the F<sub>2</sub> culture, 23P-26P, which had given the lowest percentage of the normal type and from 23P-38P in which the sex types were present in approximately equal proportions. The F<sub>3</sub> cultures derived from these are given in Table 3.

TABLE 3  
 F<sub>3</sub> progeny of open-pollinated, pistillate plants.

Culture	No. Plants	No. N	No. I	No. P	% N	% I	% P
23P-26P-1P	99	37	34	28	37.3	34.3	28.2
-2P	99	27	43	29	27.2	43.4	29.2
-3P	98	34	39	25	34.6	39.7	25.5
-4P	95	24	36	35	25.6	37.8	36.8
-5P	97	9	38	50	9.3	39.1	51.5
Total	488	131	190	167	26.8	38.9	34.2
23P-38P-1P	91	13	42	36	14.2	46.1	39.5
-2P	96	35	43	18	36.4	44.7	18.7
-3P	94	37	39	18	39.3	41.4	19.1
-4P	39	11	17	11	28.2	43.5	28.2
-5P	49	13	14	22	26.5	28.5	44.8
Total	369	109	155	105	29.5	42.0	28.4
All	857	240	345	272	28.0	40.2	31.6

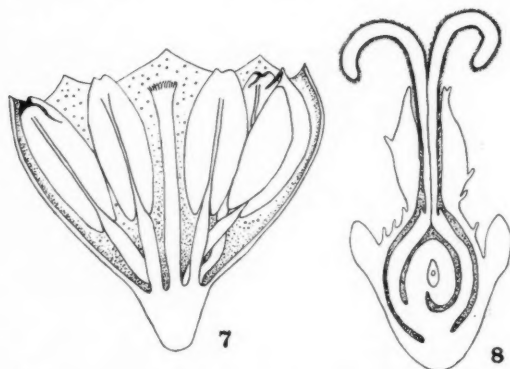


Fig. 7. Staminate flower; five stamens and a vestigial pistil.

Fig. 8. Pistillate head in longitudinal section.

Again, as in the F<sub>1</sub> and F<sub>2</sub>, all three sex types were present in each culture. However, the aggregate results show a decided decrease in pistillate plants and an increase in the normal type. A comparison of individual cultures indicates extreme variation. Derivatives of 23P-26P always yielded a higher percentage of normal and a lower percentage of pistillate plants than the F<sub>2</sub> parent, whereas, cultures derived from 23P-38P varied in both directions for each sex type compared with the F<sub>2</sub>. Selection for an increase in the frequency of pistillate plants under open-pollination was ineffectual; the percentage of pistillate plants decreased in succeeding generations and the percentage of normal plants increased.

The pistillate type in controlled crosses.

Pistillate plants of the  $F_2$  generation of strain 23P were crossed with a true-breeding normal strain, 9N, and also with intermediate segregates of 23P. These two crosses were repeated with pistillate plants of the  $F_3$  generation of strain 23P. The results are given in Table 4.

TABLE 4  
Pistillate plants crossed with a true-breeding normal strain, 9N, and with intermediate plants.

Culture	No. Plants	No. N	No. I	No. P	%N	%I	%P
P $\times$ 9N	235	42	95	98	17.8	40.4	41.7
Repeated	40	8	14	18	20.0	35.0	45.0
Total	275	50	109	116	18.1	39.6	42.1
P $\times$ I	274	44	114	116	16.0	41.6	42.3
Repeated	96	12	42	42	12.5	43.7	43.7
Total	370	56	156	158	15.1	42.1	42.7

These data indicate that the throwing of three sex types by a pistillate plant is not conditioned by the sex type of the male parent. It is peculiar that the total results from these two crosses should be so similar when the frequency of sex types under open pollination has been extremely variable. Pistillate plants have also been crossed with the unstable normal segregates of 23P, monoecious form 2, but the offspring have not as yet been grown.

## 2. THE GENETICAL BEHAVIOR OF THE NORMAL TYPE.

$F_1$  open-pollinated. (Table 5).

TABLE 5  
 $F_1$  progeny of open-pollinated, normal plants; monoecious form 1.

Culture	No. Plants	No. N	No. I	No. P	%N	%I	%P
*9N	186	186	0	0	100	0	0
100N	90	90	0	0	100	0	0
*101N	1110	1108	2	0	99.8	0.1	0
102N	99	99	0	0	100	0	0
103N	99	99	0	0	100	0	0
104N	99	99	0	0	100	0	0
*105N	25	25	0	0	100	0	0
*106N	61	61	0	0	100	0	0
107N	104	104	0	0	100	0	0
108N	97	96	1	0	98.9	1.0	0
109N	100	99	1	0	99.0	1.0	0
*110N	58	58	0	0	100	0	0
*112N	16	16	0	0	100	0	0
113N	100	100	0	0	100	0	0
114N	99	99	0	0	100	0	0
02N	97	97	0	0	100	0	0
04N	86	86	0	0	100	0	0
Total	2526	2522	4	0	99.84	0.15	0

\*All seeds produced by the parent plant were sown.  
Each culture was derived from the seed of one plant.

All cultures, except O2N and O4N, were derived from seed collected in the vicinity of Ann Arbor. Culture O2N was grown from seed collected at Fayetteville, Arkansas, through the kindness of Professor Delbert Swartz. The original seed in this case were not from one plant; from them 232 plants were grown, 98.7% normal and 1.28% of intermediate type. Culture O2N represents the offspring of one of these normal plants. Cultures O4N came from Tallahassee, Florida, from seed collected through the kindness of Professor R. M. Harper. A portion of the original seed yielded 160 plants all of the normal type. Culture O4N represents the offspring of one of these normal plants.

The data in Table 5 show that normal plants, which are so called because they are the predominant type in nature, breed quite true. The very few in-

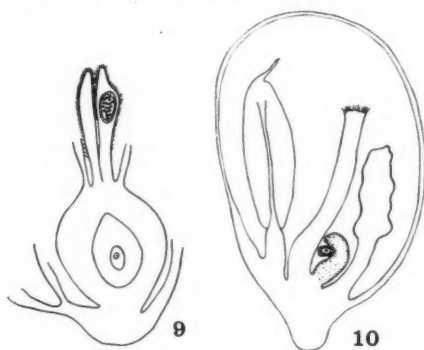


Fig. 9. Pistil with anther in style.

Fig. 10. Staminate flower with free ovule in place of stamen.

termediate plants all had preponderately staminate racemes and were probably continuous variations of the normal type. Seed from one of these plants gave 202 individuals all of which were normal. A true intermediate plant, as will be shown later in the paper, always yields normal, intermediate and pistillate plants.

F<sub>2</sub> open-pollinated. (See Table 6).

TABLE 6

F<sub>2</sub> progeny of open-pollinated, normal plants; monoecious form I.

Culture	% Germ	No. plants	No. N	No. I	No. P	% N	% I	% P
9N-1N	32.4	77	74	3	0	96.1	3.8	0
-2N	39.2	87	85	2	0	97.7	3.2	0
-3N	66.8	165	163	2	0	98.7	1.2	0
-4N	64.0	149	148	1	0	99.3	0.6	0
-5N	49.2	122	120	2	0	98.3	1.6	0
-6N	80.4	199	199	0	0	100.0	0.0	0

Culture	% Germ	No. plants	No. N	No. I	No. P	% N	% I	% P
-7N	38.4	93	92	1	0	98.9	1.0	0
-8N	62.4	149	145	4	0	97.3	2.6	0
-9N	69.2	166	166	0	0	100.0	0.0	0
-10N	40.4	101	101	0	0	100.0	0.0	0
-11N	59.6	148	148	0	0	100.0	0.0	0
-12N	69.6	172	172	0	0	100.0	0.0	0
-13N	23.6	58	58	0	0	100.0	0.0	0
-14N	42.8	103	100	3	0	97.0	2.9	0
-15N	62.4	152	152	0	0	100.0	0.0	0
-16N	58.4	146	146	0	0	100.0	0.0	0
-17N	52.4	119	117	2	0	98.3	1.6	0
-18N	66.2	152	152	0	0	100.0	0.0	0
-19N	75.2	179	178	1	0	99.4	0.5	0
-20N	83.2	192	190	2	0	98.9	1.0	0
-21N	65.6	155	154	1	0	99.3	0.6	0
-22N	76.8	176	175	1	0	99.4	0.5	0
-23N	38.4	91	91	0	0	100.0	0.0	0
-25N	36.8	79	79	0	0	100.0	0.0	0
Total	56.3	3230	3205	25	0	99.2	0.7	0

The  $F_2$  generation presented in Table 6 was derived from 24 plants selected from culture 9N; each culture in the table represents the offspring from one seed parent. The selection was from culture 9N as it was the only one available at the time, the others recorded in Table 5 were grown in subsequent years. The results obtained in the  $F_2$  generation were similar to the  $F_1$ : 3,230 plants were grown; 99.2% normal; 0.7% intermediate, all bordering on the normal type and probably continuous variations; no pistillate plants were produced.

### $F_3$ open-pollinated.

Four cultures derived from as many  $F_2$  plants were grown: culture 9N-20N-1N gave 165 plants, all normal. Culture 9N-20N-1I was the progeny of an intermediate and consisted of 202 individuals, all normal. Culture 9N-23N-1N produced 194 plants, all normal. Culture 9N-25N-1N was derived from a normal plant which grew in a row contingent to pistillate strain 23P, all the seeds were planted and out of 1,204 individuals one was intermediate and all others normal.

### Progeny of normal segregates from pistillate plants. (Monoecious form 2.)

Earlier in this paper data were given which showed that pistillate plants always produce some normal individuals; the percentage of these in open-pollinated cultures ranged from 1.7-58.0%, the average being 20.7%. These normal segregates are phenotypically identical to the true breeding normal strain. Because they do not breed true, as will be shown, they will be designated as monoecious form 2, and the true breeding strain, monoecious form 1, wherever it is necessary to distinguish between the two. It is significant that monoecious form 1 flowers earlier than the offspring of monoecious form 2. This must be taken into account in making crosses. For example, in cultures planted September 11, 1933, after eight weeks, 71% of the offspring of

form 1 were in flower, whereas, only 26% of form 2 were sufficiently mature for determination of floral types. The  $F_1$  offspring of open-pollinated plants of form 2 are presented in Table 7.

TABLE 7  
 $F_1$  progeny of open-pollinated, normal plants; monoecious form 2.

Culture	% Germ	No. plants	No. N	No. I	No. P	% N	% I	% P
23P-1N	84.8	193	85	76	32	44.0	39.3	16.5
-2N	76.0	173	85	59	29	49.1	34.1	16.7
-5N	74.4	171	95	51	25	55.5	29.8	14.6
-6N	78.4	185	95	68	22	51.3	36.7	11.8
-16N	56.4	129	61	44	24	47.2	34.1	18.5
81P-1N	46.4	109	65	36	8	59.6	33.0	7.3
-5N	80.0	194	55	110	29	28.3	56.7	14.9
-11N	71.5	139	58	79	2	41.7	56.8	1.4
150P-2N	11.6	25	13	11	1	52.0	44.0	4.0
-3N	11.2	23	16	6	1	69.5	26.0	4.3
-4N	—	118	91	22	5	77.1	18.6	4.2
23P-35P-1N	—	148	120	26	2	81.0	17.5	1.3
-2N	—	146	108	37	1	73.9	25.3	0.6
-3N	—	126	93	31	2	73.8	24.6	1.5
-4N	—	135	103	26	6	76.2	19.2	4.4
-5N	—	134	127	7	0	94.7	5.2	0.0
23P-38P-6N	—	99	57	28	14	57.5	28.2	14.1
-7N	—	96	47	34	15	48.9	35.4	15.6
-8N	—	95	57	32	6	60.0	33.6	6.3
-9N	—	93	62	23	8	66.6	24.7	8.6
-10N	—	96	56	32	8	58.3	33.3	8.3
Total		2627	1549	838	240	58.9	31.8	9.1

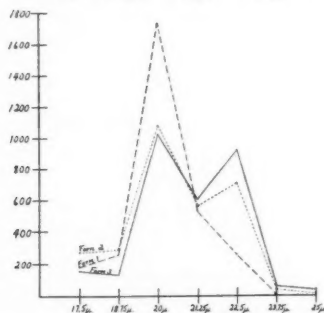


Fig. 11. Pollen measurements of monoecious form 1, 2 and 3.  
Three thousand grains measured for each.

Monoecious form 2 is very clearly unlike monoecious form 1 in its genetical behavior. (Compare Table 5 and Table 7). The latter breeds true; the former usually yields pistillate, intermediate and normal plants. Cultures derived from form 2 had a preponderance of normal plants in every instance except 81P-5N and 81P-11N. However the frequency of each sex type in a

culture was extremely variable: normal plants ranged from 28.3-94.7%; intermediates from 5.2-56.8%; pistillate plants from 0.0-18.5%.

Culture 23P-35P-5N was unique in containing no pistillate plants. This suggested the possibility of deriving monoecious form 1 from this culture. Results have been favorable; one derivative has bred true for form 1 for two generations under open-pollination. Complete data will be given on this work because the result is evidence that the female parent entirely determines the sex type in a progeny.

A pistillate individual, 23P, produced 5% normal, 21% intermediate and 72% pistillate plants. One of the pistillate segregates, 23P-35P, yielded 58% normal, 39% intermediate and 2% pistillate plants. This is the highest percentage of normal individuals ever secured from a pistillate parent. Five of the normal segregates were selected and their progeny constitute cultures 23P-35P-1N to -5N in Table 7. These were predominantly normal cultures; -5N contained no pistillate plants. Four normal plants were selected from -5N and their offspring grown with the following results: Culture 1; 204 plants, all normal. Culture 2; 98 plants, all normal except for one intermediate which approached the pistillate type and was probably not a continuous variation of form 1. Culture 3; 203 plants, all normal. Culture 4; 206 plants, 199 normal, 5 intermediate and 2 pistillate. Progeny were then grown from the normal cultures 1 and 3. Offspring from culture 3 were not all normal: One culture from an open-pollinated plant consisted of 99 plants; 95 normal and 4 intermediate. Another culture, in which the normal plant was used as a female parent crossed to an intermediate, yielded 193 plants of which 180 were normal and 13 intermediate. Seed were sown from a plant of culture 1 and gave 100 plants all of which were normal. It will be interesting to see if successive generations of culture 1 remain true to type when open-pollinated or crossed to the intermediate type.

Monoecious form 1 and 2 in controlled pollinations. (See Table 8).

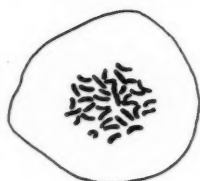
#### FIGURES

12. *A. elatior*, monoecious form 3; somatic prophase; 36 chromosomes.
13. *A. elatior*, pistillate type; somatic prophase; 36 chromosomes.
14. *A. elatior*, monoecious form 1; somatic prophase; 36 chromosomes.
15. *A. elatior*, monoecious form 1; metaphase I; 18 chromosomes.
16. *A. elatior*, monoecious form 1; metaphase II; 18 chromosomes.
17. *A. elatior*, monoecious form 2; somatic prophase; 36 chromosomes.
18. *A. elatior*, monoecious form 2; metaphase I; 18 chromosomes.
19. *A. elatior*, monoecious form 2; metaphase II; 18 chromosomes.
20. *A. trifida*; somatic prophase; 24 chromosomes.
21. *A. trifida*; metaphase I; 12 chromosomes.
22. *A. trifida*; metaphase II; 12 chromosomes.
23. *A. bidentata* x *A. trifida*; somatic prophase; 29 chromosomes.
24. *A. bidentata*; metaphase I; 17 chromosomes.
25. *A. bidentata*; metaphase II; 17 chromosomes.





12



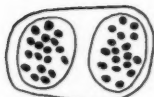
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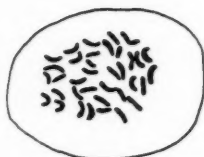
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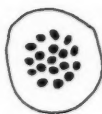
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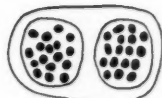
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24



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TABLE 8

Monoecious form 1 and 2 in controlled pollinations.

Culture	No. Plants	No. N	No. I	No. P	%N	%I	%P
1 selfed	106	105	0	1	99.0	0.0	0.9
2 selfed	536	287	203	46	53.5	37.8	8.5
F <sub>1</sub> (1 x 2)	157	157	0	0	100.0	0.0	0.0
F <sub>2</sub> (1 x 2)	30	30	0	0	100.0	0.0	0.0
F <sub>3</sub> (1 x 2)	41	41	0	0	100.0	0.0	0.0
2 x 1	149	61	66	22	40.9	44.2	14.7
2 x 1 (repeated)	143	55	64	24	38.4	44.7	16.7
2 from (2 x 1) x 1	83	33	32	18	39.7	38.5	21.6
1 x 3	501	501	0	0	100.0	0.0	0.0
2 x 3	98	66	20	12	67.3	20.4	12.2
3 x 1	320	60	192	68	18.7	60.0	21.2
3 x 1 (repeated)	90	20	45	25	22.2	50.0	27.7
3 from (3 x 1) x 1	97	10	49	38	10.3	50.5	39.1
3 x 2	97	63	23	11	64.8	23.7	11.3
P x 1	235	42	95	98	17.8	40.4	41.7
P x 1 (repeated)	40	8	14	18	20.0	35.0	45.0

1: monoecious form 1.

I: intermediate, monoecious form 3.

2: monoecious form 2.

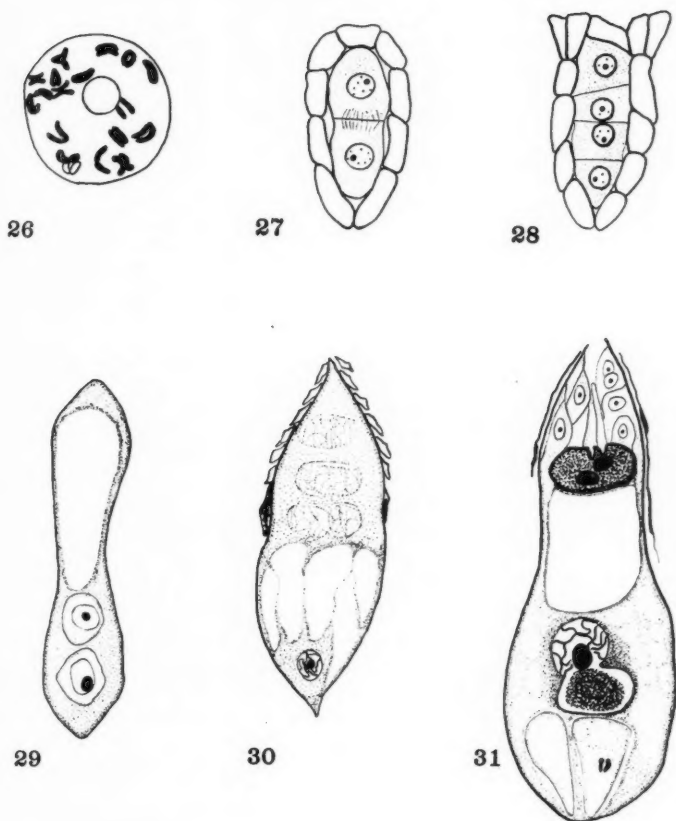
P: pistillate.

3: monoecious form 3.

N: normal (1 or 2).

The data in Table 8 indicate that whenever monoecious form 1 is used as a female parent all offspring are normal regardless of the sex type of the male parent. This is in line with the more extensive work with open-pollinated plants in which form 1 bred true for three generations. Form 2, when used as a female parent, always gave a mixed progeny consisting of normal, intermediate and pistillate plants with the last type least abundant. This duplicated the behavior of form 2 under open-pollination.

Certain data in Table 8 require comment. The one pistillate plant secured from selfing form 1 was probably a contamination; it was the first plant in the culture and may have been misplaced; no other pistillate plant has arisen among several thousand individuals derived from form 1. The ratios from selfing form 2 happened to approach the average ratios under open pollination. In the latter case 2,627 plants consisted of 58.9% normal, 31.8% intermediate and 9.1% of the pistillate type. It may seem peculiar that form 2, when used as a female parent, gave the highest percentage of normal individuals when crossed with the intermediate type. This does not mean that intermediate plants are prevaillingly normal in their genetical behavior; it will be shown that they behave quite otherwise when used as the female parent and that all genotypes behave alike when used as the male parent. The writer cannot definitely explain the high percentage of normal plants in this instance. However, individuals of form 2 may give quite different ratios when used as seed



FIGURES

26. *A. elatior*, pistillate type; diakinesis in megaspore mother cell; 18 pairs of chromosomes.
27. *A. elatior*, pistillate type; first division of megaspore mother cell.
28. *A. elatior*, pistillate type; tetrad of megaspores.
29. *A. elatior*, pistillate type; two-celled embryo sac.
30. *A. elatior*, pistillate type; four-celled embryo sac; nucellus degenerating.
31. *A. elatior*, pistillate type; mature embryo sac; several antipodals, triple fusion nucleus irregularly shaped, fusion of sperm and egg, two synergids; nucellus fragmentary.

parents and the environment can alter these ratios as will be demonstrated in another paper. The cross in question,  $2 \times 3$  and its reciprocal, gave similar, aberrant ratios; both were made at the same time with closely related plants during a different year than the other crosses were made.

c. THE GENETICAL BEHAVIOR OF THE INTERMEDIATE TYPE; MONOECIOUS FORM 3.

$F_1$  open-pollinated.

The progeny of wild, open-pollinated, intermediate plants were grown with the following results. Cultures 41, derived from one plant; 414 plants, 224 or 54.1% normal, 164 or 39.6% intermediate, and 26 or 6.2% pistillate. In addition ten cultures (3,720 plants) were grown from which incomplete data were secured. All of these cultures consisted of three sex types; normal plants comprised 17.56% of a culture.

In a culture from seed collected at Fayetteville, Arkansas, by Professor Delbert Swartz, three intermediate plants occurred among 229 plants of the normal type. One of the intermediate plants bordered on the pistillate type. All of its seed were sown with the following results: 455 plants; 125 or 27.4% normal; 330 or 72.5% intermediate; no pistillate plants. This intermediate progenitor behaved unlike any of local origin; it gave no pistillate offspring and had the highest percentage of intermediate plants ever secured. Most of the intermediates approached the normal type; only 28 were predominantly pistillate. The culture was conspicuously vigorous and flowered a month later than culture O2N (Table 5) which was derived from a normal plant in the same population.

The progeny of intermediate segregates from the pistillate type.

Pistillate plants always produce some intermediate individuals; the percentage of these in cultures under open-pollination has ranged from 23.1-58.7%, the average 39.0%. The results of growing progeny of intermediate segregates from pistillate plants are recorded in Table 9.

TABLE 9

$F_1$  progeny of intermediate segregates from the pistillate type; monoecious form 3.

Culture	%Germ	No. plants	No. N	No. I	No. P	%N	%I	%P
23P-11	41.2	97	47	32	18	48.4	32.9	18.5
-21	46.0	111	25	58	28	22.5	52.2	25.2
-101	42.8	100	48	31	21	48.0	31.0	21.0
150P-11	36.8	84	19	39	26	22.6	46.4	30.9
-21	57.2	133	61	50	22	45.8	37.5	16.5
-31	65.6	145	40	50	55	27.5	34.4	37.9
23P-38P-111	—	91	35	41	15	38.4	45.0	16.4
-121	—	94	27	47	20	28.7	50.0	21.2
-131	—	87	30	43	14	34.4	49.4	16.0
-141	—	96	38	45	13	39.5	46.8	13.5
-151	—	95	31	48	16	32.6	50.5	16.8
Total		1133	401	484	248	35.3	42.7	21.8

Each culture in Table 9 was derived from a single intermediate plant; three sex types occurred in each culture but in widely varying frequencies. In seven of the cultures the intermediate type predominated; in three cultures the normal type was most abundant, and in only culture 150P-3I the pistillate type occurred in highest frequency.

It was pointed out in the introduction that intermediate plants are extremely variable phenotypically. They range from plants which would be normal but for one pistil in one androgynous head to plants which would be pistillate but for one staminate flower. Since individual intermediate plants give variable ratios in their progeny it might be expected that predominantly pistillate plants would give a higher percentage of pistillate offspring than would predominantly normal plants. The limited data do not support this assumption. Seed were collected from five open-pollinated, intermediate plants in the same culture, 23P-38P. Three of these were predominantly pistillate and their offspring (Table 9: cultures 23P-38P-13I, -14I, -15I) together yielded 278 plants; 35.6% normal, 48.9% intermediate and 15.4% pistillate. Two of the intermediate plants were predominantly normal and their offspring (Table 9; cultures 23P-38P-11I and -12I) together yielded 185 plants; 33.5% normal, 47.0% intermediate and 18.9% pistillate. These ratios are certainly similar; the predominantly pistillate plants, oddly, gave slightly fewer pistillate individuals than did the predominantly normal plants.

Table 10 gives a résumé of the behavior of the three monoecious forms and the pistillate type under open-pollination.

TABLE 10

Résumé of genetical behavior of three monoecious forms and pistillate type under open pollination.

Female parent	No. plants	No. & % N	No. & % I	No. & % P	Range N	Range I	Range P
1	7,521	7,491 or 99.6%	30 or 0.39%	0.0 or 0%	96.1 to 100%	0 to 3.8%	0 to 0%
2	2,627	1,549 or 58.9%	838 or 31.8%	240 or 9.1%	28.3 to 94.77%	5.2 to 56.8%	0 to 18.5%
3	1,547	625 or 40.4%	648 or 41.8%	274 or 17.7%	22.5 to 54.1%	31.0 to 52.2%	6.2 to 37.9%
P	6,798	1,426 or 20.9%	2,652 or 39.0%	2,720 or 40.0%	1.7 to 58.0%	23.1 to 58.7%	2.0 to 72.8%

A massing of all data on open-pollination (Table 10) emphasizes three facts: (1) Monoecious form 1 breeds true irrespective of the pollen parent. (2) On the average the percentage of pistillate plants in a progeny is highest if the female parent is of pistillate type and decreases in the following order; female parent monoecious form 3, form 2, and form 1. (3) Individuals of a

given sex type when used as the female parent give extremely variable ratios of the sex types in their progeny (form 1 excepted).

The intermediate type (monoecious form 3) in controlled pollinations (Table 11).

TABLE 11  
The intermediate type, form 3 monoecious, in controlled pollinations.

Culture	No. Plants	No. N	No. I	No. P	% N	% I	% P
3 selfed	313	72	153	88	23.0	48.8	28.1
3 x 1	320	60	192	68	18.7	60.0	21.2
3 x 1 (repeated)	90	20	45	25	22.2	50.0	27.7
3 from (3 x 1) x 1	97	10	49	38	10.3	50.5	39.1
1 x 3	501	501	0	0	100.0	0.0	0.0
3 x 2	97	63	23	11	64.8	23.7	11.3
2 x 3	98	66	20	12	67.3	20.4	12.2
P x 3	274	44	114	116	16.0	41.0	42.3
P x 3 (repeated)	96	12	42	42	12.5	43.7	43.7

The results in Table 11 are in keeping with the more extensive work in the field under open-pollination. The intermediate type when used as a female parent, regardless of the sex type of the male parent, throws all sex types, with the intermediate individuals usually predominating. When the intermediate type is employed as a male parent the results differ from the foregoing, depending entirely on the sex type of the female parent. Throughout the investigation results indicated that the proportion of sex types in a progeny was controlled entirely by the female parent; pollen from all plants seemed to behave alike and to contribute no factors for the expression of monoecious form 2, 3 or pistillate plants. A study of the pollen grains and of the chromosomes was accordingly undertaken.

#### d. POLLEN STUDIES

Pollen grains were examined to detect possible peculiarities which might indicate why pollen of all sex types functions alike, i.e. seems never to carry factors for the expression of monoecious form 2, 3 or the pistillate type. There was no significant percentage of aborted pollen; each sex type produced less than 10% of aborted grains. The only striking peculiarity was the diversity in the size of the pollen grains; this was true of pollen from all plants so that it was necessary to make extensive measurements in order to evaluate its possible significance. A random sample of 200 pollen grains was measured from each of 15 plants of each sex type; monoecious form 1, 2, and 3. (A total of 3,000 measurements for each sex type).

The results are given graphically in Fig. 11. The measurements, in microns, are charted along the abscissa and the frequencies along the ordinate. Monoecious form 1, which breeds true for the normal type, when used as a female parent, gave essentially a normal frequency curve; the mode was 20 microns and the mean 20.14 microns. Monoecious form 2, which gives three sex types when used as a female parent, with an average of about 59% normal plants, gave a bimodal curve; the main mode 20 microns, another at 22.5

microns and the mean 20.54 microns. Form 2 had 772 grains measuring 22.5 microns or more, whereas, form 1 had only 268. Pollen measurements for monoecious form 3 gave even a more marked bimodal curve; the modes were again at 20 microns and 22.5 microns; the mean was 20.92 microns. There were 1,025 pollen grains which measured 22.5 microns or more.

The characteristic of producing large pollen grains is definitely possessed by the sex types which, when used as female parents, yield pistillate segregates. Form 1 does not produce pistillate plants and produces relatively few large pollen grains. Form 2 and 3 yield pistillate segregates; both produce a high number of large pollen grains and form 3 which yields more pistillate plants has the higher frequency of large grains. It is reasonable to assume that the large pollen grains carry factors for the expression of the pistillate type and that for some reason these grains do not function as this type is never transmitted through the male parent. The writer has no direct evidence to prove this assumption. Pollen grains of *Ambrosia elatior* L. have not been successfully germinated on some 40 nutrient media, yeast extract, stigma extracts and excised stigmas. Some technique must be devised to clear this important point.

#### e. CYTOLOGICAL STUDIES

A variation in the size of pollen grains has often been found to be proportional to chromosome number. In tulips, for example, de Mol (1928) found that the monoploid, diploid and tetraploid pollen grains show a volume ratio of 8:27:64.

Although the unusual genetical behavior and the striking differences in pollen grains in *Ambrosia elatior* L. strongly suggest diverse chromosome sets for separate sex types, my studies, up to the present, have not demonstrated chromosome differences. The  $2n$  number is 36 for all sex types and the  $n$  number 18 (Figs. 12 to 19). Meiosis proceeds without any unusual vicissitudes. The chromosomes are unfortunately very small and it is perfectly possible that there are morphological peculiarities which could be detected by an experimenter endowed with a nicer technique and capable of more critical observations.

Other species of *Ambrosia* have been cultured and, as a matter of record, have been found to possess the following chromosome numbers: *A. trifida* (Figs. 20, 21, 22)  $2n=24$  chromosomes,  $n=12$  chromosomes. *A. bidentata* (Figs. 24, 25)  $n=17$ . *A. bidentata* x *trifida* (Jones, 1933) (Fig. 23)  $2n=29$ .

Embryo sacs were studied to check on apomixis which is rather common in the *Compositae*. All sex types have been kept emasculated during the winter season, and, although they bore numerous pistillate heads, produced no seed. It is possible that pollination stimulates an apomictic development, perhaps a nucellar budding or parthenogenetic development of a diploid egg. It must be admitted that the vegetative diversity within each sex type is so great that such a possibility does not seem likely.

The development of the embryo sac has been studied in all sex types; it



is essentially normal as are the subsequent fertilization, embryo and endosperm formation. It is not easy to study the chromosomes during megasporogenesis; there is only one megaspore mother cell in a pistil and chromosome counts have been possible only at diakinesis. Fig. 26 illustrates a megaspore mother cell of a pistillate plant in the diakinesis stage. In eight instances the chromosomes are paired laterally; four bivalents are formed by chromosomes joined end to end; the members of one pair merging with the nucleolus are not in contact and could be considered as two univalents; there are five instances where only a single structure is seen, but these are, in the opinion of the writer, too large to be univalents and are believed to be bivalents in which the members are closely paired laterally.

Interkinesis following the first meiotic division is illustrated in Fig. 27 and then in turn: tetrad of megaspores (Fig. 28), two-celled embryo sac (Fig. 29), four-celled embryo sac (Fig. 30) and the mature embryo sac with syngamy occurring (Fig. 31). The nucellus degenerates early and the mature embryo sac is neatly nestled within a specialized layer of the heavy integument. As in many Compositae, (Afzelius, 1924; Schnarf, 1931) the antipodal apparatus consists of several cells. Fusion of the polar nuclei has been observed. Fig. 31 shows what is probably the endosperm nucleus shortly after triple fusion; the outline is very irregular and two large nucleoli are present.

#### Discussion

*Ambrosia elatior* L. is one of many species producing pistillate plants and also plants bearing both stamens and pistils. Often the floral types in these species have been found to be inherited but the breeding results have been complex and difficult to formulate. Undoubtedly the manner of inheritance would be clearer if the general genetical behavior for the species were better understood. The genes for floral types, and there may be many genes of graded potencies in several chromosomes, cannot very well be allocated and their phenotypic expressions traced if few or no genes for vegetative characteristics have been charted.

*Zea Mays* is unique in having many genes mapped. As a result the inheritance of floral types, though sometimes complex, can be definitely assigned to the activity of certain genes, e.g.:

Four recessive genes are each capable of producing pistillate plants; three or more recessive genes can each give rise to strains in which the individuals produce only a few or no pistillate flowers; two recessive genes are potentially able to influence the formation of two types of andromonoecious strains. (Emerson, 1924.)

If anyone feels skeptical he needs but realize that using such information it has been possible to create dioecious maize. Jones (1934) has developed one type by bringing into combination two specific sex-influencing genes whose loci are known. One of these is kept in the heterozygous condition in the male, the other is homozygous in both sexes. The interaction of both is necessary to maintain the unisexual condition. Emerson (1932) has developed two types of dioecious maize; in one of these the male is heterozygous and in the other the female.

There are monoecious species in which the sex condition is the expression of a simpler gene complex. Pastrana (1932) has made the remarkable discovery in *Begonia Schmidiana* of the presence of an unpaired chromosome which fails to enter the stem initial of a staminate flower which consequently has one less chromosome than the pistillate flower; the unpaired chromosome is probably concerned with the determination of sex. Rosa (1927) has found that in *Cucumis melo*, *C. sativus*, and *Citrullus vulgaris*, in which there are monoecious and andromonoecious varieties, the monoecious type depends upon a single dominant gene.

Sometimes the inheritance of sex does not permit a gene analysis because of the nature of the material. Hermaphrodites occur among dioecious species in which they behave as though derived from one sex. Shull (1910) found certain hermaphrodites in *Lychnis dioica* to behave like modified staminate plants. It seems to the writer that Newton's (1931) results on *Silene Otites* could be similarly explained. Here pistillate x hermaphrodite gave pistillate and staminate plants in about equal proportions, together with a very small percentage of hermaphrodites; hermaphrodite x staminate produced cultures predominantly staminate. Rosa (1925) considers the monoecious forms of spinach to be modified pistillate plants.

Numerous examples have been reported in which progeny tend to have the floral type of the female parent; this is often more pronounced the closer the female parent approaches the pistillate type. (*Mercurialis annua*, Yampolsky, 1930; *Satureja hortensis*, *Silene inflata* and *Plantago lanceolata*, Correns, 1905, 1906, 1908). Correns (1908) found that in *Plantago lanceolata* strong females crossed with hermaphrodites gave a prevailing pistillate progeny. However, by using pollen from different hermaphrodites on the same pistillate plant, it was demonstrated that the pollen parent had some influence on the proportion of sex forms in the progeny. Bartlett (1913) found that the pollen parent had equal influence in crosses between certain hermaphrodites of *P. lanceolata*.

*Ambrosia elatior*, like many of the foregoing species, has not been subjected to a general genetical analysis. It must be admitted that the inheritance of floral types, as presented in this paper, is sufficiently irregular to warrant an interpretation based on protoplasmic lability resulting in graded potencies of sex cells and consequently various graded sex expressions, such as in *Mercurialis annua* (Yampolsky, 1930). However, it seems to the writer, that the inheritance is particulate enough to hazard a tentative genetical interpretation.

Briefly, this is the proposed genetical interpretation. The expression of each of the four sex forms is controlled by the action of many genes, of differing potencies, located in several chromosomes. Monoecious form 1 is so strongly differential for its type that it behaves as though sexually homozygous. Functional male gametes of all sex forms possess the same gene complex; differential for the expression of form 1. The other forms are sexually very heterozygous. Usually a pistillate plant has a gene complex more differential for the expression of the pistillate form than has a plant of monoecious form 3 which in turn exceeds form 2. The gene complex of a male gamete, differ-

ential for form 1, may or may not be overbalanced by the pistillate complex of a female gamete because the latter will vary widely. The three forms, 2, 3 and pistillate are not to be regarded as the expression of only three definite genotypes; many genes are involved and consequently many imperceptibly graded genotypes, some strongly differential for a particular phenotypic expression, others capable of developing into any of the three sex forms depending upon the interaction with the environment.

The following evidence is given in support of the tentative genetical scheme:

(a) All functional pollen has the same effect on the proportion of sex forms in a progeny. (Therefore, all male gametes have the same gene complex for the expression of floral type.)

1. Monoecious form 1 breeds true regardless of the sex form of the male parent. This sex form was grown for three generations under open-pollination; 7,521 plants were grown and 99.6% were of form 1. Controlled crosses gave the same results. There is no evidence of apomixis.

2. A given sex form employed as a female parent gives similar ratios with different pollen parents. The data are presented in Table 12.

TABLE 12

Female parent	Male parent	No. plants	% pistillate
1	1	105	0.9
1	2	157	0.0
1	3	501	0.0
2	2	536	8.5
2	1	149	14.7
2	3	98	12.2
3	3	313	28.1
3	1	90	27.7
3	2	97	11.3
P	1	235	41.7
P	3	274	42.3

1, 2, and 3 refer to monoecious forms 1, 2 and 3; P to pistillate.

The data support the point in question except for (3 x 2) which gave far too few pistillate plants. These results were not obtained by crossing a single female parent with two pollen parents. This would be more confirmatory as plants within a sex form give variable ratios when used as a female parent. The writer has since worked out a method whereby one female parent can be so tested.

3. A strain, 23P-35P-5N, breeding true for form 1, has been developed from form 2 by selection under open-pollination. It seems unlikely that the homozygous form 1 could be so derived in a wind pollinated species if functional pollen grains carried different gene complexes for sex expression.

b. Functional pollen grains contribute only to the expression of monoecious form 1.

1. Monoecious form 1 breeds true to type regardless of the sex form of the pollen parent. If any pistillate factors are contributed by the pollen other sex forms should segregate from form 1.

2. If male gametes contribute no pistillate genes all gene complexes should become less pistillate in succeeding generations. For example, pistillate plants vary in the number and potency of their pistillate genes although they are phenotypically alike; in succeeding generations they should have fewer pistillate genes and therefore yield, in turn, fewer pistillate offspring. Data under open-pollination confirm this: pistillate plant 23P produced 531 plants of which 72.8% were pistillate. Twenty-one pistillate plants selected from the  $F_1$  yielded 3,046 plants of which 41.1% were pistillate and no progeny from a single plant gave as great a proportion of pistillate individuals as the  $F_1$ . Five pistillate plants selected from the  $F_2$  yielded 488 plants of which 31.6% were pistillate. Successive generations of monoecious form 2 agree with these results. There are no data for form 3. The relative scarcity of pistillate plants in nature is also significant; certainly these have greater survival value than all other forms which they greatly exceed in vegetative vigor and in seed production.

(c) The percentage of pistillate plants produced by the sex forms is usually in the following order: pistillate, monoecious form 3, form 2 and form 1. (Therefore the gene complexes have the same order for pistillate expression.)

The average percentage of pistillate plants under open pollination has been as follows: Pistillate form 6,798 plants, 40.0% pistillate; monoecious form 3 gave 1,547 plants, 17.7% pistillate; form 2 gave 2,627 plants, 9.1% pistillate; form 1 gave 7,521 plants, 0.0% pistillate. Results under controlled pollination were similar as Table 12 shows.

Most cultures conform roughly to the averages just given. However, individual cultures, each derived from a single plant, can be selected which yield very different results and this is a very important consideration. For example: pistillate plant 23P-35P gave 198 plants, 2.0% pistillate; monoecious form 3, plant 4I, gave 414 plants, 6.2% pistillate; form 2, plant 23P-16N, gave 129 plants, 18.5% pistillate. Here the order of pistillateness is the reverse of the foregoing and yet the cultures were sizeable.

The variability in breeding behavior and experimental evidence that the environment may influence the ratios indicate that monoecious form 2, 3 and pistillate are the expressions of numerous, imperceptibly graded genotypes. Some of the genotypes must be relatively fixed in their phenotypic expression or the average breeding results for the three sex forms in question would not be so dissimilar. Other of the genotypes must be capable of developing into any of the three sex forms depending on the interaction with the environment.

(d) Individual plants of one sex form show dissimilar ratios when pollinated by homozygous form 1. (Therefore, plants of one sex form vary in their genotypes; the gene complexes are multiple and individual genes influencing sex vary in potency.)

Five pistillate plants were pollinated by form 1 with the following results: plant no. 20 produced 19 offspring, 10.5% pistillate; no. 31 produced 57 offspring, 26.3% pistillate; no. 26 produced 18 offspring, 38.8% pistillate; no. 24 produced 37 offspring, 54.0% pistillate; no. 17 produced 104 offspring, 51.9% pistillate.

#### Summary

1. Characteristics which have been used to establish *Ambrosia elatior* L. and *A. artemisiifolia* L. as separate species are too variable in culture to justify segregation. *Ambrosia elatior* L. should be retained as it has priority of position in the Species Plantarum.

2. *Ambrosia elatior* L., in nature, is usually monoecious; there are occasional pistillate plants and plants which intergrade between the monoecious and pistillate habit. The monoecious plants, for convenience in breeding experiments, are divided in three categories.

3. Monoecious form 1, which is the prevalent form in nature, breeds true when used as a female parent. The sex form of the pollen parent in *A. elatior* never affects the nature of the offspring.

4. Monoecious form 2, which is phenotypically identical to form 1, when used as a female parent, gives on the average 10% pistillate plants.

5. Monoecious form 3, which is intermediate between form 2 and pistillate, when used as a female parent, gives on the average 20% pistillate plants.

6. Pistillate plants give on the average 40% pistillate offspring.

7. Individual cultures, with the exception of form 1, may vary widely from these averages.

8. All sex types are interfertile and all monoecious forms self fertile. There is no evidence of apomixis.

9. There is a correlation between the production of large pollen grains, presumably non-functional, and the tendency of a sex form to produce pistillate offspring.

10. The  $n$  chromosome number of all sex types is 18 and the  $2n$  number 36. There are no constant, visible differences in the chromosomes correlated with a given sex type.

11. The breeding behavior could probably be explained by a theory of protoplasmic lability resulting in graded potencies of sex cells. However, the writer favors a multiple gene interpretation because the inheritance seems to him to be particulate.

The author wishes to thank Professor H. H. Bartlett for help he has given in this study.

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# Affinities of the Flora of Indiana: Part I

Dorothy Parker

## I. Introduction

The present distribution of plants in general, depends not alone upon modern environment but also upon past conditions. The present range of any species is the resultant of its range in the past and its opportunities for subsequent migration as determined by later environmental conditions.

The disjunct occurrence of a single species having a low migration capacity indicates that it formerly covered a more extensive area and now may be considered as a relic; on the other hand the disjunct occurrence of a single mobile species sheds little light on its past history. Isolated colonies of several species are important in interpreting past conditions. It is beyond the limits of chance distribution to presume that a dozen or more species, normally growing together in a particular region should also be found together in a remote section beyond the normal limits of dispersal of any one of them.

A combination of evidence from successional tendencies and relic colonies indicates both the direction and the extent of plant migrations. The full extent may not be indicated, because the isolated colonies may have disappeared completely from the more remote parts of their original range. In such cases isolated stations of single species give some idea of their original range. The further back in time plant migrations are traced, the fewer relic colonies may be expected and the more difficult it is to reconstruct migrations.

There are approximately 1500 species of native vascular plants growing in Indiana at the present time. About sixty percent of the present flora is widespread not only in Indiana but also in a large part of eastern United States. These species are not of primary importance in this study. The remaining forty percent of the flora is of greater interest because it is made up of plants that are now isolated from the mass distribution of their species or are at the limits of their ranges. The disjunct occurrence of these species indicates that they are either withdrawing from or advancing into our area.

The present distribution of each species in Indiana was obtained from the Butler University file of maps of vascular plants which contains all of the records of distribution that have been published concerning the Indiana flora and from C. C. Deam's *Trees of Indiana* ('31), *Shrubs of Indiana* ('32), *Grasses of Indiana* ('29) and from some of Mr. Deam's unpublished records from his herbarium at Bluffton, Indiana. The community relationships were determined from field work in 1934 and 1935 and from information obtained from several publications of Indiana ecological investigations which will be mentioned later.



Only well recognized species have been used in order to eliminate false records and confusing data. The species selected are by no means all of the examples that exist in this state but the numbers were thought to be sufficient to make the illustrations clear.

The writer wishes to express her thanks to Dr. Ray C. Friesner for the use of the Butler University file of distribution maps, and Chas. C. Deam for his kindness in furnishing his unpublished data of the distribution of many herbaceous plants. She is indebted to Dr. E. Lucy Braun for suggestions and aid during the course of this work.

## II. Sequence of Events

Previous to the Pleistocene glaciation, during the Tertiary time, a rich deciduous forest including beech, tulip tree, maple, walnut, magnolia, sweet gum, sycamore, oaks and other plants, extended far north of its present boundary. This mixed deciduous forest was more widely distributed then than it is today. During this period there were oscillations in the level of the land that resulted in erosion and base leveling. These actions of uplift and depression of the surface of the earth had a profound effect upon the Tertiary flora. Doubtless some species were exterminated in these readjustments: others found on the peneplain or in the more diversified southern Appalachian region suitable habitats where they have been able to persist to the present time or from which they have spread into other favorable territory.

During late Tertiary times climatic changes caused a retreat from the north of the warm climate species resulting in a separation into more or less well defined zones. Eventually the tundra formation became the dominant vegetation in the far north. To the south of this belt was an evergreen forest while the deciduous forest took up a more southerly position.

Then the ice age began. There were at least four well defined glacial advances in America: Nebraskan, Kansan, Illinoian and Wisconsin. Illinoian and Wisconsin drifts form a mantle over seven-eighths of Indiana. Thus far evidence of other glaciation is lacking.

Slowly the ice accumulated and the glacier began to move southward into our territory. This movement was so slow that the temperate species were able to migrate, by propagules, to points far enough removed from the edge of the glaciers to be beyond the direct influence of the ice. There probably resulted a zonal arrangement of tundra at or on the margin of the ice, a band of northern coniferous forest beyond the tundra, and the intraneous flora parallel to the coniferous vegetation and farthest removed from the ice. The flora of the unglaciated region was but little disturbed by the ice mass except at the margins where the narrow zones of northern vegetation bordered the ice.

At its maximum extent the Illinoian ice occupied all but a narrow wedge of the southern part of the state (Fig. 1). However, every county but Crawford County had major streams by which the glacial waters were carried to the Ohio River, which resulted in valley trains of gravel, sand, silt, and clay from the glacier. Although this area was unglaciated, only Crawford County

(indicated by C in Fig. 1) was therefore unaffected by glaciation. The unglaciated wedge was the only place available for plant occupancy at this time. Here was assembled the intraneous flora of the region plus the northern plants that had been forced to migrate southward.

As the glacier retreated, the Illinoian drift was left, onto which plants migrated. The Illinoian drift sections that are now exposed in Indiana are almost separated by the unglaciated area (Fig. 1.). The drift varies in depth

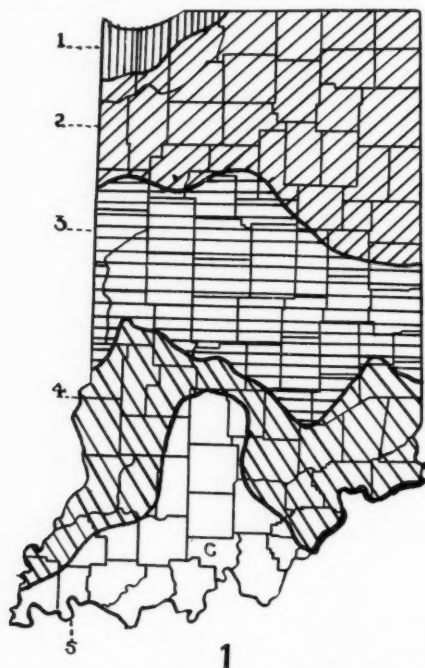


Fig. 1. Glacial Map of Indiana. (1) Lacustrine Plains. (2) Late Wisconsin Drift. (3) Early Wisconsin Drift. (4) Illinoian Drift. (5) Unglaciated Area.

over this surface from practically nothing where it has been removed by subsequent erosion, to a depth of over one hundred feet. Much of this drift-covered portion is exceptionally flat, still exhibiting the characteristics of a featureless ground moraine. Plant migrations closely followed the melting of the ice. The tundra vegetation was able to keep pace with the retreating ice border. This was followed more slowly by plants which are now found in the northern coniferous forest. A few of these plants remain at the borders of Illinoian glaciation in Indiana (Fig. 3, 4 and 60). Eventually species of the

southern deciduous forest doubtless invaded the territory. In addition to the northward migration of plants that had been restricted to the south of the ice, plants from the east and west were able to migrate into suitable habitats in the area affected by glaciation.

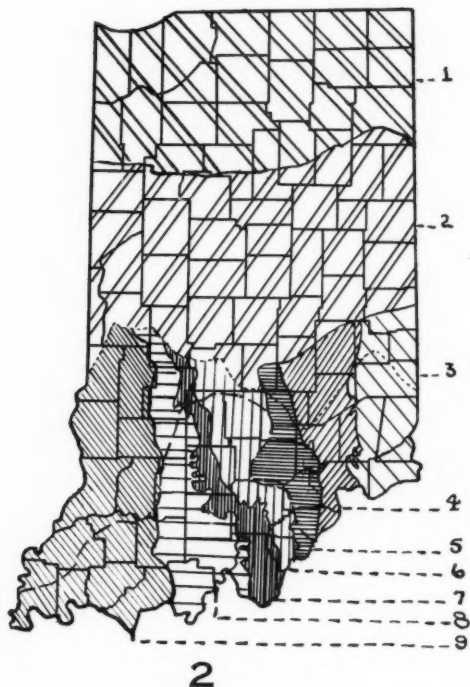
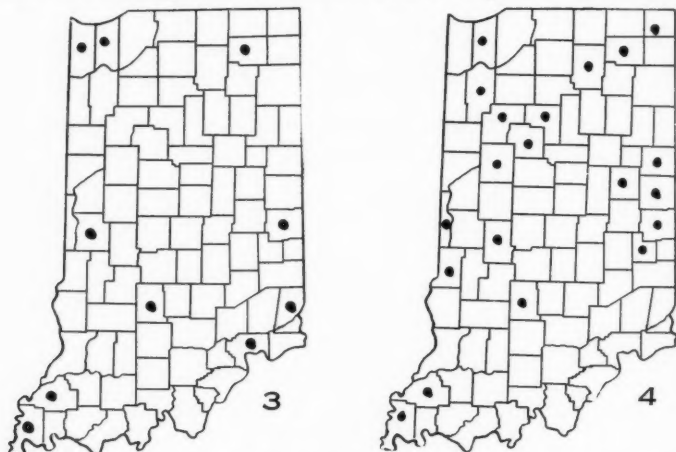


Fig. 2. Physiographic Map of Indiana Showing Regional Units based chiefly on Topographic Conditions. After Malott (1922). (1) Northern Moraine, (2) Tipton Till Plain, (3) Dearborn Upland, (4) Muscatatuck Regional Slope, (5) Scottsburg Lowland, (6) Norman Upland, (7) Mitchell Plain, (8) Crawford Upland, (9) Wabash Lowland.

The advent of the Wisconsin glacier caused another southward migration of plants. The southward extension of this glacier did not reach as far south in Indiana as did the Illinoian glacier. The intraneous flora and northern plants were crowded into the area south of the glacier as in the preceding glaciation. The Wisconsin glaciation consisted of a complex series of advances and recessions of different lobes of ice. There are several systems of moraines marking either halts or readvances of the ice border, with nearly

plane-surfaced tracts between the moraines. The Wisconsin period has been divided into Early Wisconsin and Late Wisconsin time. The portion of the state covered by Wisconsin drift contains two regional units, the Tipton Till Plain and the Northern Moraine and Lake Region (Fig. 2).<sup>1</sup> The Tipton Till Plain, including most of Early Wisconsin glaciated area and part of Late Wisconsin, is the largest physiographic division in the state, occupying nearly one-third of the entire area of the state. It is characteristically a slightly modified ground moraine plain that is monotonously flat over wide areas. The drainage lines over extensive areas of the plain are mere channels



Figs. 3 and 4. Maps showing the distribution of northern relic species whose southern stations are along the margin of Illinoian glaciation: 3. *Viola cucullata*, 4. *Lilium michiganense*.

without noticeable valley formation. The tributary streams on their approach to the great valleys developed by the Pleistocene waters are entrenched somewhat in accordance with the main valley. Such entrenchment is best developed by the streams which enter the Wabash valley. In Fountain, Montgomery and Parke counties considerable relief exists where the main streams have dissected the plain. Sugar Creek in southwestern Montgomery and northeastern Parke counties is deeply entrenched in and below the massive resistant Mansfield sandstone, and sheer cliffs of one hundred feet or more are present.

The region north of the Tipton Till Plain is the northern Moraine and Lake region, which is a compound of massive, rugged moraines occupied by lakes and broad lacustrine plains.

<sup>1</sup> The physiographic classification is that of Malott (1922) which follows that of Fenneman (1917) with some modification.

The melting glacier left vast deposits of drift containing numerous lakes and wet areas, sand plains and many other diverse habitats favorable to occupation by many different ecological groups of plants. Some of the northern plants that had been forced southward left some individuals in isolated areas in suitable habitats in the Wisconsin glacial drift as the plants moved northward again.

Since glaciation the climate has not always been the same as now. Evidence for changes in the climate have been demonstrated by Sears ('32, '35) in the study of bog pollen. By correlating studies of pollen deposits from southeastern Canada, Virginia, Iowa and Ohio, Sears has divided the post-glacial climate into the following periods: the oldest record is of a humid period followed by a period of undetermined climate, which was followed by dry, humid, dry, and finally a humid period again. The term xerothermic has been used to designate a period of mild and dry climate. The occurrence of a xerothermic period would have destroyed the balance that existed between forest and prairie vegetation with a consequent advance of the prairie vegetation eastward and a withdrawal of the mesophytic species from this area. This prairie extension persisted as long as conditions remained suitable and acted as a barrier to the migration of mesophytic species. Hence, the northward migration of mesophytic species was prevented. At the same time the northward migration of mesophytic species could continue in the east. Thus some mesophytic species were able to move around the prairie lobe and entered northern Indiana from the east. There are examples to demonstrate that such migrations actually occurred (to be described later). With a return of humid conditions the mesophytic flora invaded the territory previously occupied by more xerophytic species and the xerophytic species were able to remain only as relics in isolated stations in habitats least favorable to the invading flora. Several shifts of prairie and forest communities must have occurred with the changes from humid to dry conditions.

The vegetational history of Indiana is closely related to the geological history and climatic changes that have occurred in the past. The present flora then is the result of the readjustments in distribution that have been made by plants both in the past and at present.

The flora of Indiana as a whole is that of a mesophytic deciduous forest in which widespread intraneous species prevail. Within the state are five areas with distinctly different floras (Fig. 5).

1. The *lake region* is the northern portion of the state composed of the northern lake and moraine physiographic regional unit. Many northern plants are here and it is these that give character to the region; coastal plain and prairie species are well represented; a few Allegheny species occur.

2. The *flats* are remnants of the old Tertiary peneplain that is covered with a mantle of Illinoian drift. This area is characterized by a swamp forest in which beech, sweet gum and pin oak are the more important species (comparable to the forest of the Illinoian Till Plain of southwestern Ohio,

Braun '36). In addition to the intraneous flora there are some distinctly northern species, and some distinctly southern and Appalachian species that are at or near the limits of their ranges.

3. The *knobs* area lies in the unglaciated portion of southern Indiana in the highland region which includes the Crawford Upland, Mitchell Plain



Fig. 5. Map of Indiana showing the five areas having distinctly different floras: (1) *Lake* area, (2) *Flats* area, (3) *Knobs* area, (4) *Prairie* area (Just the main extent of prairies is mapped. Isolated communities occur in numerous counties to the east and to the south.) After Transeau (1935), (5) *Lower Wabash Valley* area.

and the Norman Upland. This highland area is a portion of the Highland Rim (Fenneman '28) and is a northwestern extension from the Appalachian plateau of Kentucky. Here occur many southern and Allegheny species along with the intraneous flora. Northern species are lacking except the few glacial relics found near the glacial boundary.

4. The *prairie* area does not correspond to a physiographic area but consists of remnants of the prairie peninsula (Transeau '35) of post-Wisconsin

age. As is to be expected prairie species are more numerous here than elsewhere in Indiana.

5. The *Lower Wabash Valley* area is a narrow strip of land bordering the Wabash River from the Ohio River northward to Vigo County. The distinctive floristic feature here is the occurrence of Mississippi embayment species.

### III. The Present Composition of the Flora

Indiana, though situated in the deciduous forest, nevertheless occupies a position more or less transitional between the northern and southern forests, the prairies, the Appalachian forest, and the Mississippi embayment region. Consequently, its flora is made up not only of large numbers of plants characteristic of the deciduous forest as a whole, but also many species having affinities with other floristic regions. However, we are more concerned with how and when the species arrived in the state than arbitrarily deciding to which floristic region each belongs.

The flora of the state is made up of widespread intraneous species, species at or near the limits of their ranges, and extraneous species. The flora then is composed of the following elements:

A. Intraneous species—general and widespread species.

B. Extraneous species and species at or near the limits of their ranges.

1. Appalachian element—composed of three groups:

a. Allegheny species<sup>2</sup>—plants which reach their maximum distribution in the Appalachian physiographic province.

b. Appalachian-Ozark species—those which reach their maximum distribution in the southern Appalachian Upland and in the Ozark Plateau.

c. Ozark species—those which reach their maximum distribution in the Ozark Plateau and adjacent areas to the west and southwest.

2. Southern element—plants whose mass distribution is in the southern part of eastern United States.

3. Northern element—plants that are characteristic of the northern part of boreal North America.

This element is made up of two groups of plants:

a. Far northern species.

b. Species of the evergreen coniferous forest region.

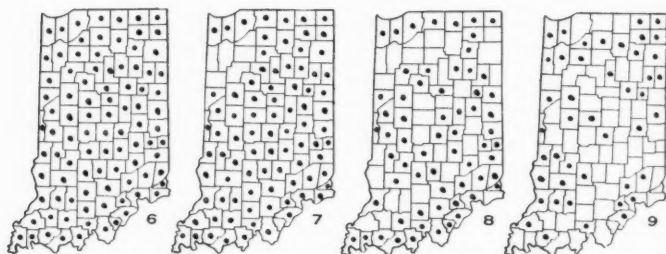
<sup>2</sup> The term Allegheny element has been used widely in floristic literature and is retained because of that reason. It does not refer to the physiographic regional unit of that name but refers to species that are widespread in the Appalachian province.



4. Prairie element—species that are characteristic of the grasslands of the western district of Interior Atlantic America.
5. Coastal Plain element—which may be divided into three groups:
  - a. Species characteristic of the northern district of the Atlantic Coastal Plain, with inland stations around Great Lakes.
  - b. Species characteristic of the Gulf Coastal Plain and Mississippi embayment district.
  - c. Species found throughout the entire Coastal Plain province.

#### A. INTRANEOUS SPECIES

Within our area are many plants that are widespread in distribution. Although important in the vegetation of the state, these plants do not reveal the past conditions of vegetation and so are not as important in a study of this type as are those of more limited distribution. Among the widespread species are *Quercus alba* (Fig. 6)<sup>3</sup>, *Acer Negundo*, *Carya cordiformis*, *Carya ovata*, *Juglans nigra*, and *Ulmus americana*. There is another large group of species generally distributed over the state but not found in every county as are the preceding species. Among these are *Fagus grandifolia* (Fig. 7), *Prunus serotina*, *Sassafras variifolium*, *Acer saccharum*, *Cornus florida* (Fig. 8), *Benzoin aestivale*, *Rosa carolina*, *Panicum huachucae*, *Panicum capillare*, *Leersia oryzoides* (Fig. 9), *Agrostis perennans*, *Elymus virginicus*.



Figs. 6-9. Widespread Species Generally distributed through Indiana. 6 *Quercus alba*. 7 *Fagus grandifolia*, conspicuous by its absence in the prairie counties. 8. *Cornus florida*. 9. *Leersia oryzoides*, its distribution being dependent upon the occurrence of wet habitats.

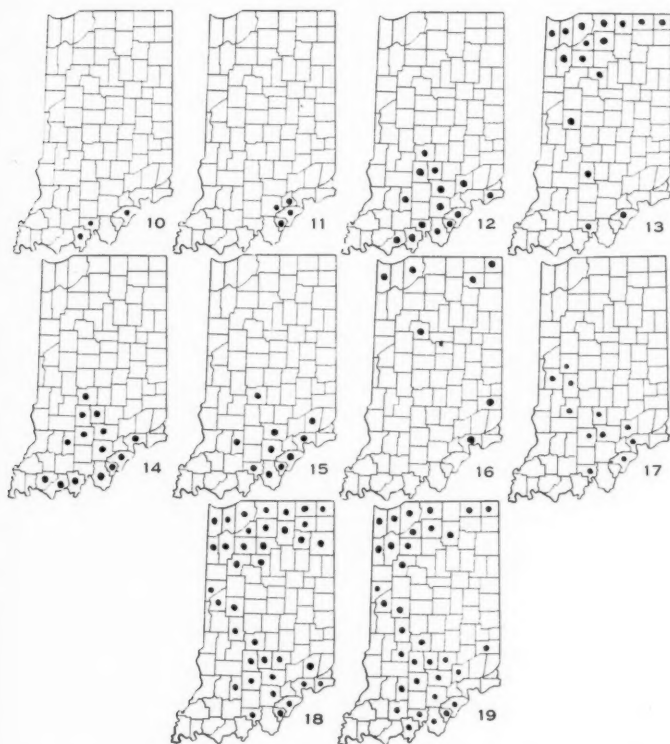
<sup>3</sup> Nomenclature is that of the seventh edition of Gray's New Manual of Botany unless otherwise noted.

## B. EXTRANEOUS SPECIES AND SPECIES AT OR NEAR THE LIMITS OF THEIR RANGES

## 1. APPALACHIAN ELEMENT

There are several species found in the knobs area of Indiana that are at the northern limits of their present distribution and attain their maximum distribution in the Appalachian province.

The Appalachian province of Harshberger ('11) is divided into the Pied-



Figs. 10-19. Alleghenian Plants in Indiana. 10. *Kalmia latifolia*. 11. *Pinus virginiana*. 12. *Vaccinium stamineum*. 13. *Gaultheria procumbens*. 14. *Quercus montana*. 15. *Castanea dentata*. 16. *Viola rostrata*. 17. *Tsuga canadensis*. 18. *Gaylussacia baccata*. 19. *Vaccinium vacillans*. Three of these records, *Castanea dentata* in Ripley Co.; *Viola rostrata* in Franklin Co.; *Gaylussacia baccata* in Ripley Co.; and *Rubus hispidus* (Fig. 82) in Ripley Co., are previously unpublished records.

mont district (which is lacking in interest floristically as far as we are concerned, the Appalachian district, and the Ozark district. The southern part of the Appalachian province, the Ozark plateau and the knobs of Indiana have had a similar geological history. Each of these has been a land area standing above sea-level since the close of the Paleozoic era; each has been uplifted and peneplained; each has escaped glaciation. The rich Tertiary flora was fairly uniform and widespread over the land area.

In Indiana, the following Alleghenian plants appear to be relics of the Tertiary flora: *Kalmia latifolia* and *Pinus virginiana* (Figs. 10-11), with a very limited distribution in southern Indiana, and *Vaccinium stamineum*, *Gaultheria procumbens*, *Quercus montana* Will., *Castanea dentata*, *Viola rostrata*, and *Tsuga canadensis* (Figs. 12-17); all of which have spread more or less into glaciated territory. *Tsuga canadensis* is generally considered a glacial relic in Indiana (Clements '34, Daubenmire '31, Friesner and Potzger '34). However, there seems to be sufficient evidence to warrant a different interpretation.

The Cretaceous and Tertiary plants of North America listed by Knowlton (1898) indicate a rather uniform flora extending from the Arctic regions through America far to the south. Hemlock was a member of this flora. The glacial period restricted the distribution of this species to the south of the glacial border in the eastern part of the United States. There were (and still are) many suitable areas in the luxuriant Southern Appalachian forest where *Tsuga* persisted. There were fewer suitable habitats outside of this region and more competition with other species; however, it is found in a few areas. Hemlock has remained in southern unglaciated Indiana as a relic of the Tertiary forest. In Indiana hemlock is established on north-facing canyon rims where there is extreme drainage and consequently dry soil (Daubenmire 1931). After its establishment, the presence of the hemlock gives rise to a secondary set of conditions which tend to inhibit the seedlings of competing plants and thus the permanency of the hemlock community is secured. In all of its stations in Indiana *Tsuga* is found on the north-facing wall at the upper rim of canyons. It has persisted in these areas that are unfavorable to the intraneous flora.

The effects of glaciation were not pronounced more than a very short distance beyond the edge of the glacier. It is not necessary to call upon glacial migrations to explain the occurrence of hemlock in Crawford and Lawrence counties. It could have persisted in these places since Tertiary time. Likewise in the stations near the border of Illinoian glaciation it has been able to persist since Tertiary time and has migrated into the glacial territory only in the habitats where it can grow due to the lack of competition with other trees.

If this species is a glacial relic that followed the retreating glaciers northward and then became widespread in the Great Lakes region, why is not hemlock pollen found in bogs of central and northern Indiana? To date

Houdek ('33) has been the only investigator to find hemlock pollen in Indiana bogs. He has found it only in very small percentages in the upper strata of peat from two bogs in the extreme northern part of Indiana, one in Porter County and the other in Steuben County. Hemlock is a prominent member of the Appalachian flora and since Pleistocene glaciation has spread north and northwest from that center into the Great Lakes-St. Lawrence Valley region where it is now a dominant in the Hemlock-White Pine-Hardwood forest of that region. This migration passed through Ohio and into Michigan but missed Indiana. The absence of pollen in the bottom of the bogs mentioned above, its scarcity in the upper part and its absence in other Indiana peat bogs south of these two indicate that this species was not a member of the northern vegetation that retreated northward with the melting glacier but that it is a Tertiary relic in unglaciated southern Indiana from whence it has spread slightly into glaciated territory since glaciation. The occurrence of hemlock pollen in the extreme northern bogs was due to the spread of some individuals from southern Michigan or eastern Ohio. Hemlock is not found at present in northern Indiana.

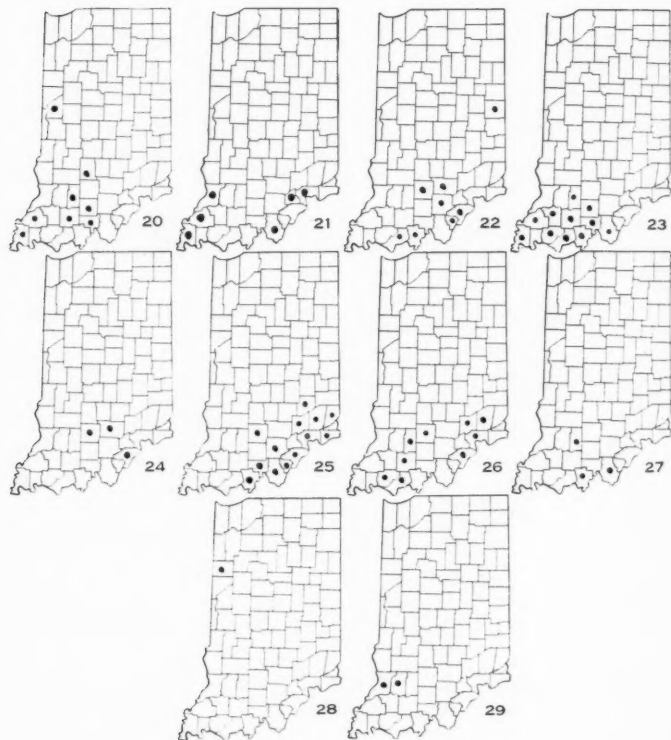
The lobe of prairie vegetation that stretched across the state in post-Wisconsin time acted as a very effective barrier to the Allegheny plants that might have been migrating northward from the knobs region so that they were restricted to the south of the prairie region. However, certain of the Allegheny plants occur not only in southern Indiana but also in the Lake region in the north. *Gaylussacia baccata*, *Vaccinium vacillans* (Figs. 18-19) and *Gaultheria procumbens* (Fig. 13) appear to have reached these northern stations by following a route from the unglaciated Allegheny plateau of eastern Ohio through the northern part of Ohio into northern Indiana.

A second group of species found in southern Indiana occurs in the southern Appalachian Upland and the Ozark plateau (Steyermark '34). Among these are *Asplenium pinnatifidum*, *Agave virginica*, *Iris cristata*, *Ulmus alata*, *Magnolia acuminata*, *Viburnum rufidulum*, *Habenaria peramoena*, *Vaccinium arboreum* (Figs. 20-27), and *Robinia Pseudo-Acacia*. The last is now found as an escape in all parts of the state but was doubtless native along the Ohio River at least in the southeastern part of the state. There is an interesting account of *Robinia* found in the book of "Western Travels" by David Thomas published in 1819.

After a traverse of three or four miles we came to Rising Sun, Indiana. . . . On leaving the river, we ascended the hills, the soil of which is very fertile, and the vegetation uncommonly fine. We had gazed at the majestic beech of this country, three feet in diameter, with branches of great size; we had seen the honey locust, the black walnut and the horse chestnut (called sweet buckeye) of equal magnitude; and here we saw, with surprise, the black locust almost a rival in stature; with grape vines like cables, hanging from tops of trees in every direction. . . .

*Cladrastis lutea*, another Appalachian-Ozark species, is native in Brown County. Deam says (in a letter of February 1936) that its habitat there leads him to believe that it will be found elsewhere in Indiana.

A third group of species are members of the group which Steyermark ('34) considers as having originated in the Ozark plateau and the adjacent area to the west and southwest. Thus, it is not surprising that only two of this group get into our area. These species are *Carex austrina* (Small) Mack and *Pentstemon tubiflorus* (Figs. 28-29). *Carex* has been reported from only Benton County, and the *Pentstemon* has been reported from both Daviess and Knox counties.

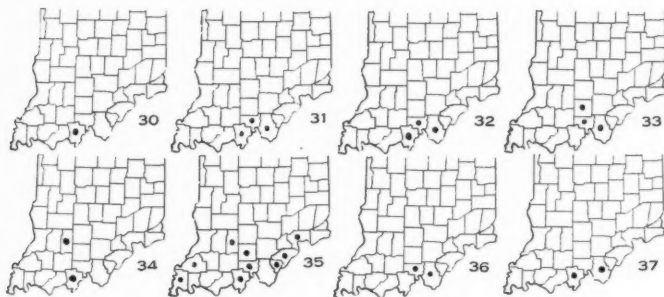


Figs. 20-27. Southern Appalachian and Ozark Species occurring in Indiana. 20. *Asplenium pinnatifidum*. 21. *Agave virginica*. 22. *Iris cristata*. 23. *Ulmus alata*. 24. *Magnolia acuminata*. 25. *Viburnum rufidulum*. 26. *Habenaria peramoena*. 27. *Vaccinium arboreum*.

Figs. 28-29. Ozark Species occurring in Indiana. 28. *Carex austrina*. 29. *Pentstemon tubiflorus*.

## 2. SOUTHERN ELEMENT

The southern element comprises those plants that are characteristic of and are widespread in the southern portion of eastern United States and which have northern stations in Indiana. Their general ranges as given in the manuals are usually from Virginia to Indiana and Illinois or Nebraska, south to Florida and Texas; or some comparable range. These southern plants show three different types of distribution in the state.

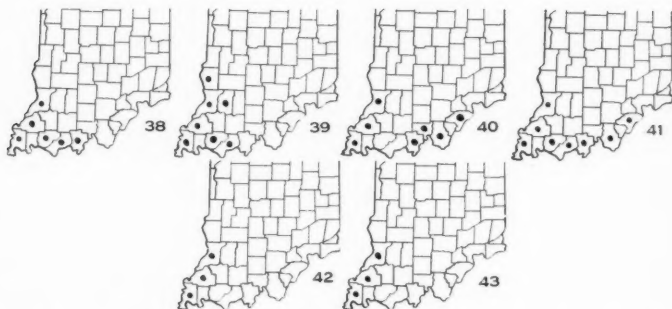


Figs. 30-37. Southern Species having a limited range of distribution in Indiana. 30. *Bumelia lycioides*. 31. *Smilax Bona-nox*. 32. *Rhamnus caroliniana*. 33. *Isoetes Engelmanni*. 34. *Cheilanthes lanosa*. 35. *Polypodium polypodioides*. 36. *Hexalectris aphylla*. 37. *Passiflora incarnata*.

The first group of southern plants is made up of species that reach their maximum distribution in the south and in Indiana are restricted to the unglaciated territory of the southern part of the state. *Bumelia lycioides* (Fig. 30) is considered one of the rarest shrubs of Indiana. It has been reported from only one station near a perpendicular cliff along the Ohio River in Perry County. *Smilax Bona-nox* (Fig. 31) has been reported from open woodlands along the bluffs of the Ohio River from Perry, Crawford and Harrison counties. *Rhamnus caroliniana* (Fig. 32) occurs in Harrison, Crawford and Perry counties near the Ohio and Blue rivers where it is locally frequent on wooded slopes from the base to the top of the ridges. *Isoetes Engelmanni*, *Cheilanthes lanosa*, *Polypodium polypodioides*, *Hexalectris aphylla* and *Passiflora incarnata* (Figs. 33-37) are other southern plants with a limited distribution in particular habitats in southern Indiana. *Jussiaea decurrens* has been reported from only Posey and Spencer counties and *Spigelia marilandica* in Posey County. This portion of the state was largely unaffected by glaciation, therefore it has been possible for these plants to live here undisturbed for a long period of time since this is the oldest land area in the state.

A second group of southern plants is composed of species that inhabit borders of streams and river bottoms in southern Indiana. They have moved into the glaciated region a short distance. *Adelia (Foresteria) acuminata*.

*Quercus lyrata*, *Bignonia capreolata*, *Arundinaria macrosperma*, *Aristolochia tomentosa* and *Vitis palmata* (Figs. 38-43), are found along the margins of the Ohio and Wabash rivers and their tributaries. This type of distribution has been attained by migration of the species into our area from the south where they have found continuous suitable habitats along the margin of the Mississippi and Ohio rivers.



Figs. 38-43. Southern Species that have crossed the glacial border in Indiana. 38. *Adelia acuminata*. 39. *Quercus lyrata*. 40. *Bignonia capreolata*. 41. *Arundinaria macrosperma*. 42. *Aristolochia tomentosa*. 43. *Vitis palmata*.

The last group of southern plants is made up of species that have extended their ranges beyond the unglaciated into the glaciated portion of the state. Some species such as *Symphoricarpos orbiculatus*, *Diosyros virginiana* and *Hydrangea arborescens* (Figs. 44-46) have made considerable advance and extend into the Wisconsin glaciated territory. Other species as *Evonymus americanus*, *Aralia spinosa*, *Smilax glauca*, *Phoradendron flavescens*, *Ascyrum hypericoides*, *Asclepias perennis*, *Salvia lyrata* and *Liquidambar styraciflua* (Figs. 47-54), have extended their ranges into the Illinoian drift area but their ranges are terminated at or near the Wisconsin glacial boundary. On the other hand *Aesculus octandra* (Fig. 55) is found only in Dearborn, Jefferson, Clark, and Crawford counties and in no place more than a mile from the river, hence it is found but a very short distance within the limits of Illinoian glaciation.

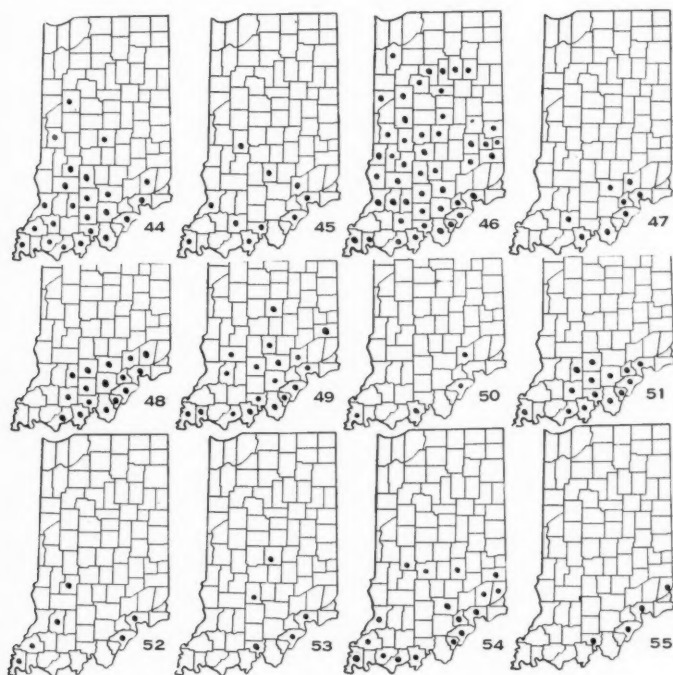
### 3. NORTHERN ELEMENT

As mentioned previously, the boreal relics of Indiana can be divided into two main groups: (a) far northern species, and (b) species of the northern evergreen coniferous forest region. The first of these can be further subdivided into circumboreal species and species confined to boreal North America.

Naturally the number of circumboreal plants in our region is limited. *Schizachne purpurascens* (Torrey) Swallen (Fig. 56) has been reported from

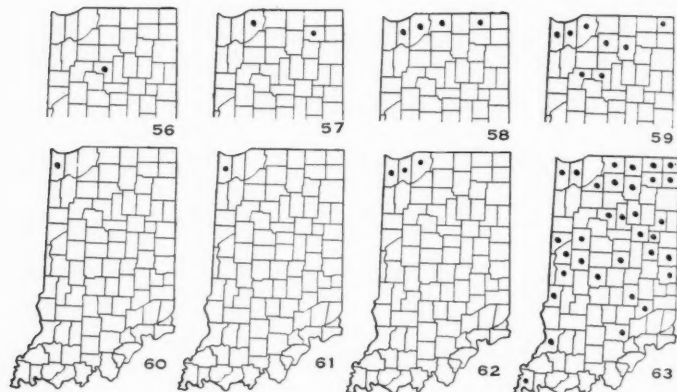


Cass County. It occurs in dry, moist, or rocky woods and open places in North America from Labrador to Alaska, south in the United States to Pennsylvania, Kentucky, Indiana, South Dakota and Montana and in the mountains from British Columbia to New Mexico; Siberia and Japan. This grass becomes rare in the southern part of its range. *Calla palustris* (Fig. 57) inhabits cold bogs from Nova Scotia to New Jersey, west to northern Indiana, Minnesota and northward; also in Eurasia. This plant has become quite rare in Indiana due to its destruction by man and now occurs in only two counties in extreme northern Indiana. *Vaccinium Oxycoccus* (Fig. 58) is circumboreal in its general distribution and occurs infrequently in northern Indiana in bogs. *Campanula rotundifolia* (Fig. 59) likewise is circumboreal in its distribution with a few southern stations in northern Indiana. *Pyrola chlorantha*



Figs. 44-54. Southern Species that have extended their ranges some distance within the glacial boundary. 44. *Symphoricarpos orbiculatus*. 45. *Diospyros virginiana*. 46. *Hydrangea arborescens*. 47. *Evonymus americanus*. Fig. 48. *Aralia spinosa*. 49. *Smilax glauca*. 50. *Phoradendron flavescens*. 51. *Ascyrum hypericoides*. 52. *Asclepias perennis*. 53. *Salvia lyrata*. 54. *Liquidamber styraciflua*. 55. *Aesculus octandra*.

(Fig. 60) also is circumboreal and has been reported from extreme north-western Indiana.



Figs. 56-60. Circumboreal Species occurring in Indiana. 56. *Schizachne purpurascens*. 57. *Calla palustris*. 58. *Vaccinium Oxycoccus*. 59. *Campanula rotundifolia*. 60. *Pyrola chlorantha*.

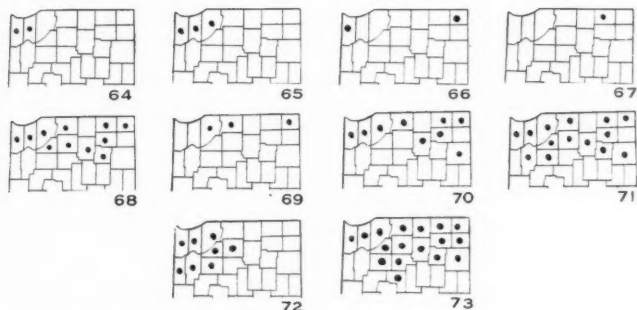
Figs. 61-63. North American Boreal Species occurring in Indiana. 61. *Shepherdia canadensis*. 62. *Arctostaphylos Uva-ursi* var. *coactilis*. 63. *Caltha palustris*.

Some of the far northern plants found in Indiana are confined to boreal North America. Among these are *Shepherdia canadensis* (Fig. 61) found only in Lake County; *Arctostaphylos Uva-ursi* var. *coactilis* Fernald (Fig. 62) (a variety of the species found in Eurasia) is found on rocks and bare hills in the far north of America and as far south as Virginia, Illinois, Colorado and northern California. With one exception it is, in Indiana, confined strictly to the dunes near Lake Michigan. It is found in open places on the crests and slopes of dunes. It has already become quite scarce in Lake and La Porte counties, but is still frequent in most parts of Porter County (Deam '32). *Corydalis sempervirens* ranges in the north from Nova Scotia to Alaska and occurs in Lake, Newton, Pulaski, and Starke counties. *Caltha palustris* (Fig. 63) is more widespread than these others and occurs as far south as the glacial border.

Present disjunct stations of plants of the conifer forest region now separated from the mass of the species and the remains of tamarack in deposits of glacial age (Coulter and Thompson '86) are evidence that boreal vegetation actually occurred in southern Indiana.

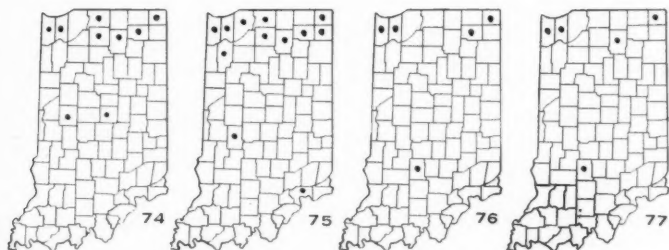
Numerous members of the northern forests are found in the state. One

— group of these species is now found only in the extreme northern portion of the state. Among these are *Thuja occidentalis*, *Pinus Banksiana*, *Glyceria borealis*, *Poa paludigena* Fern. and Wieg., *Salix candida*, *Sorbus subvestita* Greene, *Rhamnus alnifolia*, *Betula pumila*, *Myrica asplenifolia* and *Larix laricina* (Figs. 64-73).



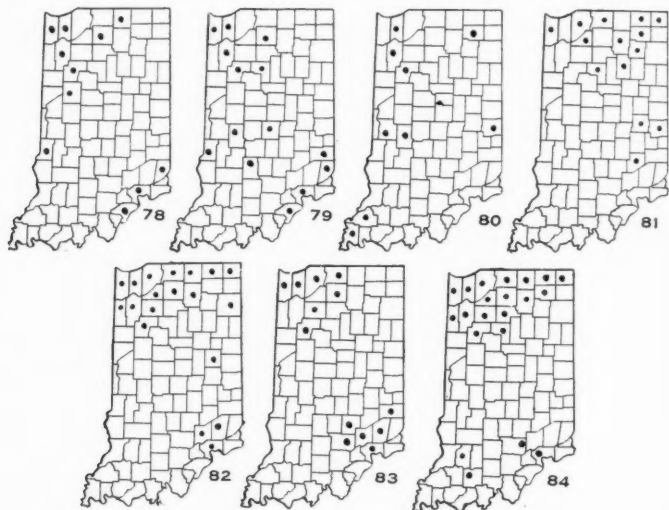
Figs. 64-73. Species of the Northern Evergreen Coniferous Forest Region now found only in the extreme northern part of Indiana. 64. *Thuja occidentalis*. 65. *Pinus Banksiana*. 66. *Glyceria borealis*. 67. *Poa paludigena*. 68. *Salix candida*. 69. *Sorbus subvestita*. 70. *Rhamnus alnifolia*. 71. *Betula pumila*. 72. *Myrica asplenifolia*. 73. *Larix laricina*.

A second group of species of the northern evergreen forest region is made up of those having several northern Indiana stations with disjunct occurrences at or near the glacial boundary. Among these are *Cypripedium hirsutum* Mill. (*C. reginae*), *Maianthemum canadense*, *Pyrola americana* and *Pyrola elliptica* (Figs. 74-77). The occurrence of the *Pyrolas* in Monroe County was in the old "Lake Flatwoods" area.



Figs. 74-77. Species of the Northern Evergreen Coniferous Forest Region found in northern Indiana with disjunct stations near the glacial border. 74. *Cypripedium hirsutum*. 75. *Maianthemum canadense*. 76. *Pyrola americana*. 77. *Pyrola elliptica*.

A third group of the northern evergreen forest is found in northern Indiana and in scattered suitable habitats as far south as the margin of Illinoian glaciation. Among these are *Viola lanceolata* (Fig. 78), *V. cucullata* (Fig. 3), *Houstonia caerulea* (Fig. 79), *Symplocarpus foetidus* (Fig. 80), *Lilium michiganense* (Fig. 4), *Potentilla fruticosa*, *Rubus hispidus*, *Vitis labrusca*, and *Spiraea tomentosa* (Figs. 81-84).



Figs. 78-84. Species of the Evergreen Coniferous Forest Region found in northern Indiana and in scattered suitable habitats as far south as the margin of Illinoian glaciation. 78. *Viola lanceolata*. 79. *Houstonia caerulea*. 80. *Symplocarpus foetidus*. 81. *Potentilla fruticosa*. 82. *Rubus hispidus*. 83. *Vitis labrusca*. 84. *Spiraea tomentosa*. (Note the localization of the last three in the flats.)

With the changes to drier climatic conditions during post-Wisconsin time, the prairie barrier extended across the state and separated the northern plants near the glacial border from the ones in the northern part of the state, hence many of this group tend to be somewhat localized in the southern part of the drift areas, particularly in the southeastern Illinoian flats where numerous suitable habitats are found (Figs. 82-84). Comparable distributions of these species are seen in Ohio (Braun '35).

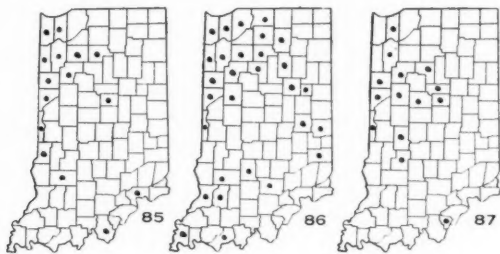
#### 4. PRAIRIE ELEMENT

At present the prairie communities of Indiana are restricted largely to the western portion of the central and northern part of the state with small isolated communities to the east and northeast. Many species of the prairie

flora have a wide range of distribution and occur far beyond the limits of the grassland formation. Single occurrences of these species of wide range would have little significance. However, the former more widespread extent of grassland is indicated by communities which appear in habitats comparable to those in the western prairies and in which the species bear the same relationships to each other (as to relative importance and dominance) as they do in the prairie region.

As the Wisconsin glacier melted, the present Great Lakes were formed. At first they were more extensive and stood at higher levels. Lake Chicago, the predecessor to Lake Michigan, extended far south of the present lake. As new outlets were formed, the lake gradually retreated toward the north. The newly formed sandy beaches and shores were available not only to the species migrating from the south, but were suitable and available to the prairie species of the west and also to the Coastal Plain species of the east. The post-Wisconsin eastward shift of the prairie margin formed a peninsula of this vegetation reaching southern Michigan and central Ohio (Transeau '35). With the return of more humid climatic conditions, the deciduous forest invaded this peninsula. Gradually the forest replaced the prairie vegetation at the margins of the peninsula except in the more extreme habitats. It is in these places that prairie communities are still found and it is these relics that indicate the former extent of the prairie migrations.

The prairie communities are of two types, wet and dry, i.e., they correspond to the lowland prairies dominated by the big bluestem grass, and the upland prairies dominated by the little bluestem grass, as described by Weaver and Fitzpatrick '35. Of the twenty most important forbs of the wet prairie species (having a 10% or higher occurrence as a society of the first class in the lowland prairies), the greatest number are of wide distribution. They occur not only in the prairie region but range far east, some of them appearing locally in the forest region as well. Among these are *Galium tinctorium*, *Fragaria virginiana*, *Steironema ciliatum*, *Aster salicifolius*, *Anemone canadensis*, *Solidago altissima*, *Phlox pilosa*, *Helianthus grosseserratus*, *Zizia aurea*,



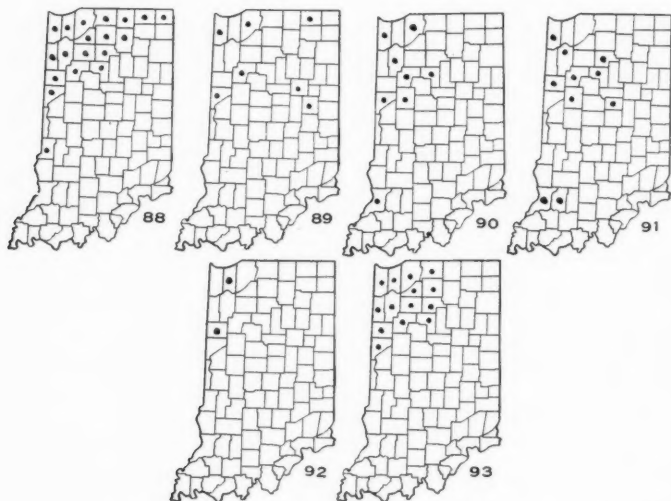
Figs. 85-87. Three of the most important forbs of the wet prairies of Central United States reach the eastern limits of their distribution in or near Indiana. 85. *Silphium laciniatum*. 86. *Silphium integrifolium*. 87. *Asclepias sullivantii*.

*Teucrium canadense*, *Viola papilionacea*, *Pycnanthemum virginianum*, *P. flexuosum*, *Veronica virginica*, *Asclepias verticillata*, and *Cicuta maculata*.

Only three of the twenty important forbs of the wet prairies are at or near their eastern limits of distribution in Indiana. These are *Silphium laciniatum*, *S. integrifolium*, and *Asclepias Sullivantii* (Figs. 85-87).

The grasses of both wet and dry prairies are quite widespread, in some cases ranging as far south as Mexico and South America.

The nineteen most important forbs of the dry prairies (having from 10-74% occurrence as a society of the first class in the upland prairies), have a more limited distribution than the wet prairie species. A few are widespread and are found as far east as the Atlantic coast in suitable habitats. These are *Aster multiflorus*, *Erigeron ramosus*, *Euphorbia corollata*, *Solidago rigida* and *Liatris scariosa*. However, a larger percentage of the most important forbs of the dry prairies are at or near their eastern limits of distribution in Indiana. These species are *Amorpha canescens*, *Helianthus rigidus* (Cass) Desf., *Petalostemum candidum*, *P. purpureum*, *Brauneria pallida*, and *Coreopsis palmata* (Figs. 88-93). The remainder of the nineteen most important dry prairie forbs reach their eastern limit of distribution to the west of Indiana and so do not enter our flora.



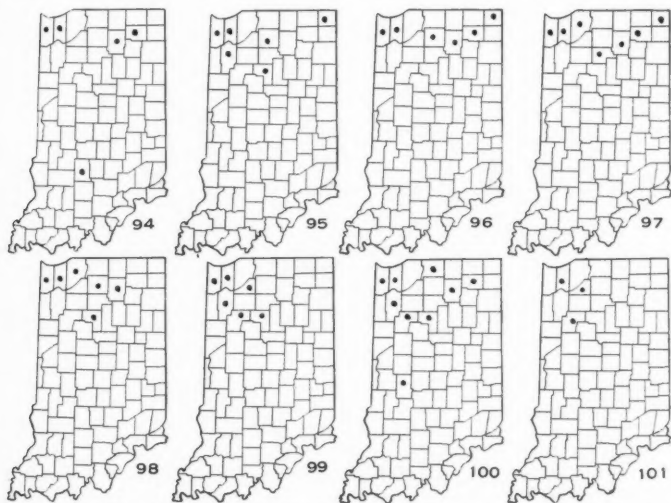
Figs. 88-93. Six of the most important forbs of the dry prairies reach the eastern limits of their distribution in or near Indiana. 88. *Amorpha canescens*. 89. *Helianthus rigidus*. 90. *Petalostemum candidum*. 91. *Petalostemum purpureum*. 92. *Brauneria pallida*. 93. *Coreopsis palmata*.

## 5. COASTAL PLAIN ELEMENT

The Coastal Plain species which occur in Indiana are found either in the lake region or in the Lower Wabash and Ohio River valleys or in both regions.

The distribution of these coastal plain species within Indiana and their general distribution outside of the state show that they have had three possible routes along which they could migrate; (1) by way of the old Mohawk-Hudson outlet of the glacial Great Lakes; (2) by way of the Ottawa connective (another outlet of the glacial Great Lakes); (3) by way of the Mississippi embayment. Some arrived, perhaps more or less simultaneously, by way of the Mohawk-Hudson outlet and the Mississippi embayment. As the Wisconsin ice sheet melted away from what is now the lake region, sand barrens, swales and lagoons were far more extensive than at present. These conditions afforded a more or less continuous suitable habitat for the coastal plain plants from the Atlantic coastal plain to our region, by way of the Mohawk-Hudson connective and the Ottawa connective (Peattie '22).

A considerable number of coastal plain species more or less scattered over the northern part of Indiana appear to have arrived by way of the Mohawk-Hudson outlet of the glacial Great Lakes. Among these are *Bartonia virginica*, *Polygala cruciata*, *Utricularia gibba*, *Hydrocotyle umbellata*, *Xyris flexuosa*, *Sisyrinchium atlanticum*, *Lupinus perennis*, and *Viola primulifolia*,



Figs. 94-101. Atlantic Coastal Plain Species occurring in northern Indiana. 94. *Bartonia virginica*. 95. *Polygala cruciata*. 96. *Utricularia gibba*. 97. *Hydrocotyle umbellata*. 98. *Xyris flexuosa*. 99. *Sisyrinchium atlanticum*. 100. *Lupinus perennis*. 101. *Viola primulifolia*.



(Figs. 94-101). The disjunct occurrence of *Bartonia virginica* in Monroe County is explained by Potzger ('34) as a chance distribution effected by birds since this station is in a newly formed bog and it could not be a relic of glaciation.

On the basis of its distribution, it seems probable that *Ammophila breviligulata* Fernald (Fig. 102) has entered the state by way of the Ottawa connective. It is found at the head of Lake Michigan. Outside of the state it is found on sandy shores along the Atlantic coast from Newfoundland to North Carolina and inland along the St. Lawrence river system to the Great

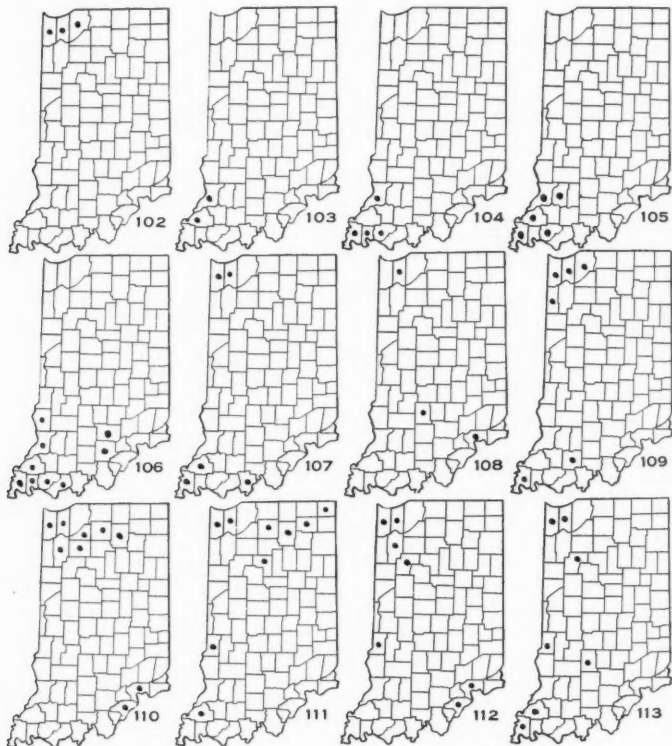


Fig. 102. *Ammophila breviligulata*, of the north Atlantic Coastal Plain and Great Lakes Region. 103-107. Mississippi embayment Species reaching their northern limits of distribution in Indiana. 103. *Gleditsia aquatica*. 104. *Taxodium distichum*. 105. *Ilex decidua*. 106. *Celtis mississippiensis*. 107. *Crotalaria sagittalis*. 108-113. Coastal Plain Species found in the Lake region in northern Indiana, and along stream margins and valleys in southern Indiana. 108. *Linum striatum*. 109. *Styrax americana*. 110. *Rhexia virginica*. 111. *Peltranda virginica*. 112. *Rotala ramosior*. 113. *Fimbristylis autumnalis*.

Lakes. Peattie ('22) lists it as occurring on the shores of Lake Ontario, in the region of Lake Erie, Saginaw Bay (Lake Huron), Detroit and St. Clair rivers, Lake St. Clair and Port Huron. It is not found in the Hudson-Mohawk Valley or the Finger Lakes region.

Certain species in Indiana are limited to the lower Ohio and Wabash valleys. These are represented by *Gleditsia aquatica*, *Taxodium distichum*, *Ilex decidua*, *Celtis mississippiensis* (*C. laevigata*) and *Crotalaria sagittalis* (Figs. 103-107). These species are conspicuous members of the flora of the coastal plain region that extends up the Mississippi Valley to southern Illinois. This Mississippi embayment region is an alluvial plain and is continuous with the alluvial plain of the Ohio River and the Lower Wabash River in southwestern Indiana. Thus there is a continuous suitable habitat for these coastal plain species into southern Indiana.

A fourth group of coastal plain species is found in the lake region in northern Indiana and southern Indiana along stream margins and in the valleys. Among these are *Linum striatum*, *Styrax americana*, *Rhexia virginica*, *Peltandra virginica*, *Rotala ramosior* and *Fimbristylis autumnalis* (Figs. 108-113). The last two species have comparable distributions in Ohio. The distribution of these species in northern Indiana and northern Ohio has been achieved by migration along the Mohawk-Hudson connective, while the distribution in southern Indiana and in southern Ohio can be explained by migration along the stream margins of the Mississippi and Ohio river systems from the southern coastal plain. *Peltandra* being present in northern and southern Indiana and only in northern Ohio adds weight to this explanation.

#### IV. Summary

Approximately sixty percent of the flora is intraneous, the remaining forty percent is composed of extraneous and species that are at or near the limits of their ranges. This forty percent of the flora is divided into five main groups that have affinities with five distinct floristic regions: Appalachian, Southern, Northern, Prairie and Coastal Plain. In general the Appalachian species represent relics of the Tertiary flora and are found, in the main, in the unglaciated knobs region of the state; a few have spread into glaciated territory. The southern species reach the northern limits of their ranges in Indiana. The northern species are relics of glacial migrations. The prairie species are remnants of the post-Wisconsin prairie peninsula. In general, the Coastal Plain species are relatively recent entrants in the flora of the state. Certain Mississippi embayment species are at the limits of their ranges. Such diversity in the flora can not be explained on the basis of present conditions, therefore geological history and climatic changes have been called upon in order to trace the vegetational history of the state.

The present discussion has been concerned chiefly with individual species. This section will be followed by Part II which will be concerned with studies of communities in which are found extraneous species and species that are at or near the limits of their ranges.

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# The Composition and Structure of an Oak Woods, Cold Spring Harbor, Long Island, with Special Attention to Sampling Methods\*

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## Introduction

The author has had an opportunity to study certain oak woods, in which *Quercus montana* is dominant or codominant, in Tennessee, Indiana, and New York. Certain strikingly similar aspects of these widely separated woods led to a detailed investigation of their composition and structure with the purpose of ascertaining their similarities and differences. This is the first of three reports.

At this time also it is of interest to compare three methods of sampling the tree layer. The three sampling methods may be called: 1) the single plot method, 2) the strip method, 3) the scattered plot method. By each method a total of 2,500 sq. m. was sampled. This total area was, in each case, built up on a basis of 25 quadrats each 10 x 10 m. In the single plot method (or square method) the 25 quadrats were arranged in a square 50 x 50 m. An effort was made to locate this square plot so as to be representative of the total area of the woods considered (about 15.5 acres). In the strip method the 25 quadrats were laid on a line, forming a strip 10 x 250 m. The strip was run from north to south through the woods, essentially across the relief, so as to sample both hill and ravine sites. In the scattered method the 25 quadrats were spaced 50 m. apart on center in a checkerboard pattern, sampling 4 per cent of the woods considered.

The woods here described occupies morainal hills immediately west of First Lake, Cold Spring Harbor, on the north shore of Long Island about 30 miles east of New York City. This general morainal region is one dominated vegetationally by the climatic climax group known to most American ecologists as the oak-chestnut association. For a consideration of the salient vegetational and environmental features the reader is referred to Conard, 1935.

## General Description

Referring first to the tree layers, we find that the woods is definitely

\* Contribution from the Botanical Laboratories of the University of Tennessee. N. Ser., No. 3.

dominated by species of oak: *Quercus montana*, *Q. velutina*, and *Q. borealis maxima*. The latter two species were not kept separate in some of the quantitative studies because of the difficulty of distinguishing the larger trees in the absence of fruit or twigs. Although no earlier quantitative studies are available, it is nevertheless evident that the chestnut, *Castanea dentata*, was once an important codominant with oak previous to the ravages of the chestnut blight.

The following 18 species of trees compose the arborescent layers, nomenclature after Sudworth, 1927: *Acer rubrum* L., *Amelanchier laevis* Wieg., *Betula lenta* L., *Castanea dentata* (Marsh.) Borkh., *Cornus florida* L., *Fagus grandifolia* Ehrh., *Hicoria alba* (L.) Britt., *H. glabra* (Mill.) Sweet, *Quercus alba* L., *Q. borealis maxima* (Marsh.) Ashe, *Q. montana* Willd., *Q. velutina* Lamarck, *Sassafras variifolium* (Salisb.) Kuntze, together with 5 species unencountered in the sampling by quadrats; *Betula populifolia* Marsh., *Fraxinus americana* L., *Nyssa sylvatica* Marsh., *Prunus serotina* Ehrh., *Robinia pseudoacacia* L. Of the 18 species, 3 fall into a layer dominated by *Cornus florida*. Neither of the 2 associates, *Amelanchier laevis* and *Betula populifolia*, is of any importance what so ever.

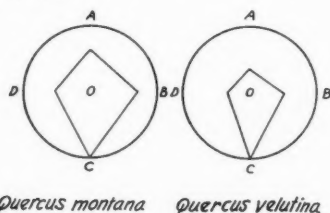


Fig. 1. Phytophographs for the tree dominants.

In the superior tree layer only 3 species are of importance, 2 of which are lumped together as already mentioned. Fig. 1 gives phytophographs for the dominants. The data for the construction of the phytophographs are presented in the following notes, based on the scattered method:

- AO: Per cent of total density of trees 10 in. d.b.h. or over:  
*Q. montana* 63,      *Q. velutina* 37
- BO: Per cent frequency of trees 10 in d.b.h. or over:  
*Q. montana* 72,      *Q. velutina* 56
- CO: Per cent of four size classes represented (these data are amplified in the following paragraph):  
*Q. montana* 100,      *Q. velutina* 100
- DO: Per cent of total basal area:  
*Q. montana* 54,      *Q. velutina* 34.

With respect to (CO) the distribution through the size classes, the following density data for the species are of interest, based on the scattered method:

	Less than 1 in. d.b.h.	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. and over d.b.h.
<i>Quercus montana</i> -----	xxx	75	25	38
<i>Quercus velutina</i> -----	—	9	3	22
<i>Acer rubrum</i> -----	xxx	71	12	—
<i>Betula lenta</i> -----	x	9	13	—
<i>Cornus florida</i> -----	xxx	79	4	—
<i>Hicoria alba</i> -----	—	3	—	—
<i>Castanea dentata</i> -----	x	7	—	—
<i>Quercus alba</i> -----	—	2	1	—
<i>Amelanchier laevis</i> -----	—	1	—	—
<i>Fagus grandifolia</i> -----	—	2	1	—
<i>Hicoria glabra</i> -----	—	3	2	—
<i>Sassafras variifolium</i> -----	—	2	—	—



Fig. 2. A general view of the *Quercus* phytocoenosis showing the inferior tree layer of *Cornus*.

It is apparent that *Q. velutina* is very poorly represented by reproduction, considering the number of large trees present. It is equally apparent that *Q. montana* is strongly represented by trees in all age classes, in fact, it is the only species of the superior arborescent layer so represented. In the inferior arborescent layer *Cornus florida*, the dominant, also enjoys a strong reproduction. *Castanea dentata* is represented only by a few sprouts which become blight infected and die before they attain any size. The remaining species have a spotty reproduction and show no indication of playing an increasingly important role in the woods.

The third layer is dominated by the evergreen mountain laurel, *Kalmia latifolia*, which, in many places, attains a coverage of almost 100 per cent, and frequently a height of 3 meters or more. Altogether there are 12 species of shrubs and 5 species of woody vines in the flora, none of which attains any considerable coverage or serious competition with *Kalmia*. In fact about one-third of the shrubs belong more properly in the herbaceous layer (field layer) as also do the vines. The latter are capable of climbing to considerable heights but apparently in this woods the moisture relationships are not suitable as they are characteristically prostrate. Following is a list of the species, nomenclature after Taylor, 1915: Vines; *Parthenocissus quinquefolia* (L.) Planch., *Smilax rotundifolia* L., *Toxicodendron Toxicodendron* (L.) Cockerell, *Vitis aestivalis* L., *V. Labrusca* L., and the shrubs; *Azalea nudiflora* L., *Gaylussacia baccata*



Fig. 3. A general view of the *Quercus* phytocoenosis showing the tall shrub layer of *Kalmia*.

(Wang.) C. Koch, *G. frondosa* (L.) T. & G., *Kalmia latifolia* L., *Rosa* sp? (sterile), *Rubus allegheniensis* Porter (?), *R. hispidus* L., *Vaccinium vacillans* Kalm., *V. vicinum* Bicknell (?), *Viburnum acerifolium* L., *V. Canbyi* (Rehder) Britt. (?), *V. prunifolium* L.

*Kalmia latifolia* alone forms a very definite layer throughout most of the woods. While making a survey of the timber plots notes were taken on the coverage class of *Kalmia* in each plot.



	Square method	Scattered method
Less than 1% or absent -----	1 plot	2 plots
Coverage class 1 (1-5%) -----	no plots	2 plots
Coverage class 2 (6-25%) -----	1 plot	3 plots
Coverage class 3 (26-50%) -----	6 plots	4 plots
Coverage class 4 (51-75%) -----	9 plots	5 plots
Coverage class 5 (76-100%) -----	8 plots	9 plots
Average, coverage class 4 -----	(60%)	(55%)

The characteristic presence of this evergreen shrub is taken as one of the main criteria for Conard's (1935) forest association, *Quercetum prinii kalmietosum*. (Note that *Quercus prinus* of authors is not *Q. prinus* L., the former being properly designated as *Q. montana* Willd.)

There is a certain correlation between the distribution of *Kalmia* and *Q. montana* in the present woods: The two usually occur together. Also, both of them usually occur on slightly less favorable sites than the other species of oak in the woods, on hill tops, upper slopes, etc. The more mesophytic species, *Betula lenta* and *Fagus grandifolia* occupy the more favorable sites, bottoms of small draws, lower north-facing slopes, etc.

Although the herbaceous layer includes 57 species, 8 of which are ferns, it is exceedingly fragmentary and only very locally forms closed communities. Such patches are usually in the bottoms of the more mesophytic ravines where *Kalmia* is absent or of low coverage, or in openings along paths. In fact, throughout the woods as a whole where the *Kalmia* layer is well developed large stretches may be completely barren of herbs or only with scattered plants of *Unifolium canadense*. A list of all herbaceous plants observed follows, nomenclature after Taylor, 1915:

PTERIDOPHYTA: *Adiantum pedatum* L., *Athyrium Filix-foemina* (L.) Roth. (?), *Botrychium obliquum* Muhl., *Dennstaedtia punctilobula* (Michx.) Moore, *Dryopteris marginalis* (L.) A. Gray, *D. noveboracensis* (L.) A. Gray, *Lycopodium complanatum* L., *Polystichum acrostichoides* (Michx.) Schott.

SPERMATOPHYTA: *Actea alba* (L.) Mill., *Agrostis alba* L., *Aralia nudicaulis* L., *Aster divaricatus* L., *Carex cephaloidea* Dewey (?), *C. pennsylvanica* Lam., *C. Swanii* (Fern.) Mack., *C. virescens* Muhl., *Chimaphila maculata* (L.) Pursh, *Collinsonia canadensis* L., *Corallorhiza maculata* Raf., *Cunila origanoides* (L.) Britt., *Dasytoma flava* (L.) Wood., *Deschampsia flexuosa* (L.) Trin., *Epigaea repens* L., *Fissipes acaulis* (Ait.) Small, *Fragaria virginiana* Duchesne (?), *Galium circaezans* Michx., *G. trifolium* Michx., *Geranium maculatum* L., *Geum canadense* Jacq., *G. vernum* (Raf.) T.&G., *Hieracium paniculatum* (L.) Britt., *Hypopitys americana* (DC.) Small, *Hypoxis hirsuta* (L.) Coville, *Juncoides campestre* (L.) Kuntze, *Lespedeza repens* (L.) Britt., *Lobelia inflata* L., *Lysimachia quadrifolia* L., *Meibomia nudiflora* (L.) Kuntze, *Mitchella repens* L., *Monotropa uniflora* L., *Nabalus trifolialis* Cass., *Panicum Ashei* Pearson, *P. commutatum* Schult., *Peramium pubescens* (Willd.) MacM., *Polygonatum biflorum* (Walt.) Ell., *Potentilla* sp? (sterile), *Pyrola americana* Sweet, *Solidago caesia* L., *S. bicolor* L., *Tovara virginiana* (L.) Raf., *Unifolium canadense* (Desf.) Greene, *Uvularia perfoliata* L., *Vagnera stellata* (L.) Morong, *V. racemosa* (L.) Morong, *Veronica officinalis* L., *Viola triloba* Schwein., *Washingtonia Claytoni* (Michx.) Britt.

The 33 bryophytes found in the woods are listed in the accompanying Table 1. Many rather extensive patches of soil are dominated by clumps of *Leucobryum glaucum* and *Dicranum scoparium*. Most frequent on bark are

species of *Plagiothecium* and *Hypnum*. The species on stones are not strictly epipetric, but are able to grow on the stones by virtue of a thin layer of soil, probably having followed lichens on the stones. Three liverworts and six species of mosses occur exclusively on bark. Four species occur on both bark and soil.

No effort was made to identify the lichens, but they are rather unimportant in this woods. Neither were the fungi and algae considered.

The following brief summary presents the distribution of the 125 species

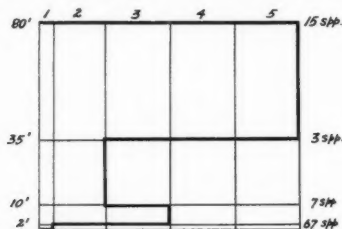


Fig. 4. A coverage-stratification diagram giving the approximate height and the number of species for each layer. The heavy line on the right indicates the coverage class in each layer.

of the flora according to certain life-form and taxonomic divisions. Fig. 4 gives a diagrammatic representation of the natural stratification of the phytocoenosis and of the coverage in each synusia.

Summary of the flora of a small oak woods (about 15 acres studied).

Woody Plants	Trees	18	
	Vines	5	
	Shrubs	12	35
Herbaceous plants	Flowers	49	
	Ferns	8	57

TABLE 1

Bryophytes<sup>1</sup> of a small oak woods west of First Lake, Cold Spring Harbor, classified according to substratum.

Liverworts	Soil	Bark	Stone
<i>Bazzania trilobata</i> (L.) S. F. Gray	x	x	
* <i>Scapania nemorosa</i> (L.) Dumort	x		
* <i>Calypogeia Trichomanis</i> (L.) Corda	x		

\* Species so marked were not mentioned by Conrad (1935) in his general discussion of the forests of this type.

<sup>1</sup> Determinations checked by A. J. Sharp, University of Tennessee.

Mosses	Soil	Bark	Stone
* <i>Cephalozia lunulaefolia</i> Dumort -----	x		
* <i>Cephalozia bicuspidata</i> (L.) Dumort -----	x		
* <i>Nardia crenulata</i> (SM.) Lindb. -----	x		
* <i>Geocalyx graveolens</i> (Schrad.) Nees -----	x		
* <i>Lophocolea minor</i> Nees -----		x	
* <i>Lophocolea bidentata</i> (L.) Dumort -----		x	
* <i>Lophocolea heterophylla</i> (Schrad.) Dumort -----		x	
* <i>Ptilidium pulcherrimum</i> (Web.) Hampe -----		x	
Mosses			
<i>Thuidium delicatulum</i> (L., Hedw.) Mitt. -----	x	x	x
<i>Plagiothecium elegans</i> (Hook.) Sulliv. -----	x	x	
<i>Dicranum montanum</i> Hedw. -----	x	x	
<i>Polytrichum Ohioense</i> R. & C. -----	x		
* <i>Pogonatum brevicaulis</i> (Brid.) Beauv. -----	x		
* <i>Ditrichum pallidum</i> (Schreb.) Hampe -----	x		
<i>Pohlia nutans</i> (Schreb.) Lindb. -----	x		
<i>Dicranella heteromalla</i> (L.) Schimp. -----	x		
<i>Dicranum scoparium</i> (L.) Hedw. -----			x
<i>Dicranum flagellare</i> Hedw. -----	x		
<i>Catharinea angustata</i> Brid. -----	x		
* <i>Catharinea undulata</i> (L.) W. & M. -----	x		
* <i>Mnium hornum</i> L. -----	x		
<i>Georgia pellucida</i> (L.) Rabenth. -----	x		
<i>Leucobryum glaucum</i> (L.) Schimp. -----	x		
<i>Heterophyllum Haldanianum</i> (Grev.) Kindb. -----	x		
<i>Hypnum reptile</i> Michx. -----		x	x
<i>Hypnum imponens</i> Hedw. (log) -----		x	
* <i>Plagiothecium denticulatum</i> (L., Hedw.) Bry. Eur. -----		x	
* <i>Mnium medium</i> B. & S. -----		x	
<i>Homomallium adnatum</i> (Hedw.) Broth. -----		x	
* <i>Amblystegium Juratksanum</i> Schimp. -----		x	
<i>Brotherella recurvans</i> (Michx.) Fleisch. -----	x <sup>2</sup>		
Number of species: (total, 34) -----	24	14	3
Bryophytes -----			
Liverworts -----	11		
Mosses -----	23		
			34

126 species

## Statistical Results and Discussion

The results from the 3 sampling methods are compared in a series of tables. Table 2 shows the total basal area in sq. ft. for each species, and per cent which that basal area is of the whole for each survey based on 2,500 sq. m. each (about 0.62 acres). The three species of oak collectively consti-

<sup>2</sup> This is the only species mentioned by Conrad which was not collected from the woods here studied.

tute 79 per cent of the basal area for the square method, 82 per cent for the strip method, and 88 per cent for the scattered method. In the square method *Quercus montana* was shown to be of less importance than *Q. velutina* (with *Q. borealis maxima*). In the other two methods the reverse was true. Considering the strip and scattered methods, which are more reliable for the woods as a whole, *Q. montana* constitutes about one-half of the stand and the other two oaks about one-third of the stand. The results for the associated species are more or less uniform for all surveys and none plays an important role in the superior tree layer.

Table 3 gives the total density per 2,500 sq. m. of each species for each survey together with the percentage which that density is of the whole. In parenthesis is given the density of trees 10 in d.b.h. or over. *Quercus montana* consistently exceeds the other oaks in density because of the small number of little trees of that species. *Acer rubrum* has a density out of proportion to its basal area percentage due to the small number of trees attaining the larger size groups. *Cornus florida* has a high density and a relatively low basal area due to its life-form. It is, however, the sole dominant in its layer. Examining the data of this table and that on construction of phytographs, it would appear that *Q. montana* is destined to increase its percentage composition at the expense of the other oaks and associated species. Although *Acer rubrum* shows strong reproduction it is evident that its survival value in the older ages is low. One would not expect it generally to increase its percentage composition in the superior layer. None of the species now playing a minor role in the superior tree layer shows a strong reproduction indicative of a tendency towards increasing its role. Specifically, there is no indication that the more mesophytic species like *Fagus* and *Quercus alba* indicate any successional tendency. *Betula lenta* shows a higher reproduction but is too small a species to become a codominant in strong competition with the older oak trees.

While measuring the trees on the strip survey the crown coverage was indicated for each species on each 10 x 10 m. quadrat (segment of the strip). It is interesting to compare the results of the ocular crown estimate with the percentages obtained from total basal area. Take *Quercus montana*, the most important species, as revealed by the survey:

Cover class 1 (1-5% coverage) .....	1	10 x 10 m. plot
Cover class 2 (6-25% coverage) .....	5	10 x 10 m. plots
Cover class 3 (26-50% coverage) .....	4	10 x 10 m. plots
Cover class 4 (51-75% coverage) .....	3	10 x 10 m. plots
Cover class 5 (76-100% coverage) .....	9	10 x 10 m. plots
Absent .....	3	10 x 10 m. plots
Average, high class 3 (48%) for .....	25	10 x 10 m. plots

TABLE 2

A comparison of three methods of sampling a small oak woods.

Species	Square <sup>1</sup>		Strip <sup>2</sup>		Scattered <sup>3</sup>	
	Basal area	%	Basal area	%	Basal area	%
<i>Quercus montana</i> -----	11.06	21.0	27.29	46.1	38.74	53.6
<i>Quercus velutina</i> -----	31.27	58.0	21.34	36.0	24.88	34.4
<i>Acer rubrum</i> -----	5.26	9.7	5.35	9.0	2.94	4.1
<i>Betula lenta</i> -----	3.82	7.1	1.53	2.6	2.96	4.1
<i>Cornus florida</i> -----	1.65	3.1	2.42	4.1	1.42	2.0
<i>Hicoria alba</i> -----	.11	—	.95	1.6	.02	—
<i>Castanea dentata</i> -----	.06	—	.08	—	.04	—
<i>Quercus alba</i> -----	.55	1.0	.07	—	.36	—
<i>Amelanchier laevis</i> -----	—	—	.07	—	.01	—
<i>Fagus grandifolia</i> -----	—	—	.14	—	.10	—
<i>Hicoria glabra</i> -----	.03	—	—	—	.78	1.1
<i>Sassafras variifolium</i> ----	.09	—	.06	—	.01	—
Total basal area -----	53.90		59.24		72.25	

1 2,500 sq. m. (50 x 50 m.) tallied by 100 sq. m. quadrats.

2 2,500 sq. m. (10 x 250 m.) tallied by 100 sq. m. quadrats.

3 2,500 sq. m. (10 x 10 m.) quadrats spaced 50 m. on center.

4 This method was used last and *Quercus velutina* and *Q. borealis* maxima were tallied separately, but here the results are united for the sake of comparison with the earlier failure to distinguish the two species.

TABLE 3

A comparison of three sampling methods on a small oak woods.

<i>Quercus montana</i> -----	521 (8) <sup>2</sup>	17	124 (24)	28	138 (38)	36
<i>Quercus velutina</i> -----	29 (26)	9	34 (16)	8	34 (22)	9
<i>Acer rubrum</i> -----	81 (2)	26	110	25	83	22
<i>Betula lenta</i> -----	32 (2)	11	26	6	22	6
<i>Cornus florida</i> -----	89	29	127	28	83	22
<i>Hicoria alba</i> -----	3	1	5 (1)	1	3	1
<i>Castanea dentata</i> -----	7	2	8	2	7	2
<i>Quercus alba</i> -----	1 (1)	—	2	—	3	1
<i>Amelanchier laevis</i> -----	—	—	1	—	1	—
<i>Fagus grandifolia</i> -----	—	—	1	—	3	—
<i>Hicoria glabra</i> -----	2	—	—	—	5	1
<i>Sassafras variifolium</i> ----	6	2	6	1	2	—
Totals 1 in. d.b.h. and over	302		444		384	
Totals 10 in. d.b.h. and over	39		41		60	

1 Density, 1 in. d.b.h. and over.

2 Density, 10 in. d.b.h. and over.

Compare this with the basal area table and we find that this exact method revealed 46 per cent of the total basal area for *Quercus montana*. *Acer rubrum* was given class 2 on a basis of the ocular estimate and had 9 per cent on the basal area basis (class 2). *Quercus velutina* was estimated at class 2 (averaging 16 per cent) but on a basis of basal area it showed up in class 3 (36 per cent). This discrepancy can be explained by reference to the table on density where we see that about 50 per cent of the black oak trees were 10 in. d.b.h. or over, whereas only about 20 per cent of the mountain oak trees were 10 in. d.b.h. or over. It was obvious that trees of the understory (smaller than 10 in. d.b.h.) account for an inordinate amount of the total crown coverage. Younger trees being much less numerous for the black oak, its crown cover was naturally estimated at a lower class. The case of *Cornus florida* is interesting. It was estimated at class 2, but despite having 127 individuals its basal area was only 4 per cent of the total. This discrepancy arises from the fact that *Cornus* really belongs to a separate synusia, that of the inferior tree stratum, and its basal area should be considered separately from that of the superior arborescent stratum. All other species fell into class 1 (or even less than 1 per cent in most cases) by each method. It would seem then that there is a close relation between percentage of total basal area and percentage of total crown cover, especially if the separate layers are considered. This matter, however, needs extensive investigation. It seems to me that the relations between crown cover and basal area of species would be apparent only when the study is based on natural layers. Furthermore, it would seem that they should approximate each other when the crown is closed but that such might not be the case in open stands. Most inferior layers are open stands and individual differences in crown shape have more of a chance to produce a discrepancy between crown cover and basal area.

In Table 4 the figures of the first column represent an effort to place the species in the order of their importance. This is entirely subjective estimation after walking around in the woods. The percentages of the second column represent an effort at quantitative estimation for the woods as a whole. The figures of the third column represent crown cover estimates made in 25 10 x 10 quadrats arranged in a strip. The percentages of the last column are based on basal area derived from the strip survey.

There is a rather remarkable correspondence between the various estimates and the basal area determination in the preceding table with respect to the dominant species, *Quercus montana*. Reference to the results of the square method reveals a quite different percentage for this species (21 per cent). This is due, of course, to the narrow range of the sample, a block 50 x 50 m. If located elsewhere, such a block might have shown even less *Quercus montana* or more of that species—well up toward 100 per cent. On a basis of the scattered quadrats the percentage (53 per cent) is again quite close to the other estimates.

The figures for *Quercus velutina* (including *Q. borealis maxima*) show a good correspondence on a basis of basal area by the strip and the scattered method, but for the square method *Q. velutina* was correspondingly as high

as *Q. montana* was low. *Acer rubrum*, *Betula lenta*, and *Cornus florida* are three remaining species of any importance in the composition of the tree layer. Of these, *Acer rubrum* is apparently somewhat more important among

	Estimated order	Crown cover, entire woods	Crown cover on strip	Basal area on strip
<i>Quercus montana</i> -----	1	45%	Class 3 (48%)	46% (3)
<i>Quercus velutina</i> -----	2	25%	Class 2 (16%)	36% (2)
<i>Betula lenta</i> -----	3	5%	Class x	3% (1)
<i>Quercus alba</i> -----	4	5%	Class x	x
<i>Acer rubrum</i> -----	5	5%	Class 2	9% (2)
<i>Fagus grandifolia</i> -----	6			x
<i>Hicoria glabra</i> -----	7	x	Class x	x
<i>Hicoria alba</i> -----	8	x	Class x	2% (1)
<i>Castanea dentata</i> -----	9	x	Class x	x
<i>Fraxinus americana</i> -----	10	x	Class x	x
<i>Cornus florida</i> -----	1	15%	Class 2	4% (1)
<i>Sassafras variifolium</i> -----	2	x	Class x	x

mesophanerophytes while *Cornus florida* is dominant in the microphanerophyte layer. It falls into class 1 coverage on a total basal area basis but as it does not exceed 5 in. d.b.h., nor the microphanerophytic layer, the basal area basis does not reveal its true importance in its own layer where it is dominant with a coverage of class 2.

From the foregoing considerations it is apparent that equal sample areas give a better sample of the whole woods by the strip method than by the square method and likewise the scattered method seems to be the best of all three. In the strip method the line of continuous samples was run across the topographic features, that is across the low hills and ravines, so that all sites were sampled. Likewise, in the scattered method all sites were sampled. However, in the square method, due to the limited extent of the area sampled (50 x 50 m.) one is likely to sample only one site. If the various sites (and various chance compositions of the woods) are each sampled by such a square one gets a picture of the whole woods, as in the instance of the smaller and scattered quadrats, but on a more adequate basis because the total sample area and the various minor differences in composition then become greater, some of which are related to differences in site. The choice between the three methods depends ultimately then on what one desires to illustrate and the time one has to devote to the study.

In the present woods (about 15.5 acres, sampled 4 per cent by the scattered method) the composition is not homogeneous. Ridges carry a heavier stand of *Quercus montana* and more mesophytic lower slopes, especially when north-facing, carry little or no *Q. montana* and a greater admixture of the more mesophytic species (*Fagus grandifolia*, *Betula lenta*, etc.) Fig. 5 shows the relationship of *Q. montana* to topography. In the second and third quadrats of the strip several large trees of *Q. montana*, which had recently died,



reduced what otherwise would have been a normal upper slope stand of that species. Its absence or low basal area in quadrats 6-9 and 12-15 correlates well with topography. The strip and scattered method each sample the woods as a whole while the square method is capable of sampling (on an equivalent area) only one such condition. If the investigator considers that the differences in composition from place to place deserve recognition (as separate forest types, or as *locies*) then each distinct composition (if on a site basis) deserves separate sampling. This can be accomplished, however, on a basis of the strip

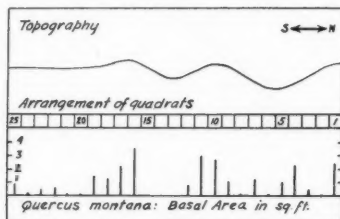


Fig. 5. The relationship of *Quercus montana* to topography along the strip.

method or the scattered method if one notes the topographic situation of each small quadrat taken and then lumps the results from similar sites. This is essentially the method of foresters when preparing cover type maps from strip surveys.

Table 5 shows the frequency of the species based on the three surveys. There are considerable differences for the more frequent species, Classes C, D, and E, as determined by the three methods. It is obvious that no great dependence is to be placed on any more than a general frequency indication. In other words, 5 classes of frequency offer sufficiently close designation in this type of community, with no significance attachable to differences of a few per cent.

On a basis of the square method, frequency was determined for tree reproduction, other woody species, and for herbs. The results are given in Table 6. Certain facts are obvious. *Kalmia*, which has a high coverage, also has a high frequency. This is to be expected on the basis of plots 10 x 10 m. Within the area three other shrubs have a frequency in class D but are of low coverage. Among the trees it is evident that reproduction is not abundant and general since the frequencies are so generally low. Among herbs only *Unifolium* has a high frequency and its coverage is quite low, hardly being in class 1 most of the time. Considering the size of the quadrats, which is relatively very large for herbs, it is evident that the herbaceous layer is poorly developed—open and fragmentary. In fact, this condition made a special study of the herbaceous layer unnecessary.

Table 7 presents a survey of the life-form distribution of the flora. In comparing this phytocoenosis with Raunkiaer's "normal spectrum" one notices

immediately the number of hypogaeal species (Hy) which exceed the normal by 19 per cent, and the low representation, in fact almost complete absence, of therophytes. It seems to the writer that interesting results will be obtained by such life-form statistics as data accumulate in the literature allowing the comparison of the same, or closely related, phytocoenoses from widely separated localities.

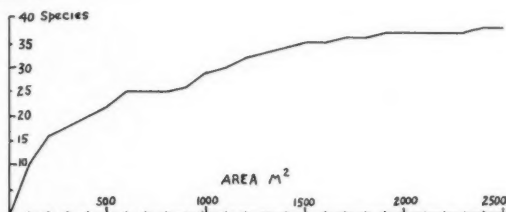


Fig. 6. The species-area curve based on the square method and all species.

The last consideration in this paper is that of the relation between species and area. Fig. 6 presents such a curve based on the square method and all species. After the practice of Braun-Blanquet and others this curve may be taken to indicate a minimum-area around 2,000 sq. m. for this phytocoenosis as a whole. Fig. 7 gives curves based only on trees 1 in. d.b.h. and over for the three sampling methods. The scattered method quickly gives an almost complete sampling of species with the maximum number at 1,400 sq. m. (12 species, the same as for 2,500 sq. m.) and 10 of the 12 species at an area of only 300 sq. m. One would conclude that for the tree layer of the woods

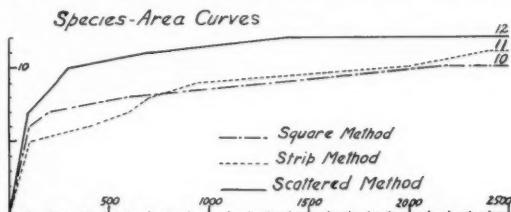


Fig. 7. Species-area curves for all three methods based on trees 1 inch d.b.h. and over.

as a whole the minimum-area is around 1,500 sq. m. If, however, the various sites are sampled separately by the square method one may conclude that a 500-600 sq. m. sample is adequate. The strip method, having neither the dispersal of the scattered method nor the concentration of the square method, gives a much less satisfactory species-area curve. Once again the indication is that the choice between methods depends on whether one considers the sites, with their corresponding composition, as units. In the latter case the square method is to be recommended, in the former case the scattered method.

TABLE 5

A comparison of three methods of sampling a small oak woods.<sup>1</sup>  
Frequency percentages based on 25 quadrats, each 10 x 10 m.

Species	Square	Strip	Scattered
<i>Quercus montana</i> -----	68	88	96
<i>Quercus velutina</i> -----	60	68	80
<i>Acer rubrum</i> -----	84	92	78
<i>Betula lenta</i> -----	56	40	44
<i>Cornus florida</i> -----	76	84	60
<i>Hicoria alba</i> -----	12	12	8
<i>Castanea dentata</i> -----	16	28	24
<i>Quercus alba</i> -----	4	8	12
<i>Amelanchier laevis</i> -----	-	4	4
<i>Fagus grandifolia</i> -----	-	4	8
<i>Hicoria glabra</i> -----	4	-	16
<i>Sassafras variifolium</i> -----	16	12	8
Number of species: F-Class A -----	5	5	6
F-Class B -----	0	2	1
F-Class C -----	2	0	2
F-Class D -----	2	1	2
F-Class E -----	1	3	1

<sup>1</sup> These frequencies are based only on trees 1 in. d.b.h. and over.

TABLE 6

Frequency of species on 25 quadrats at 10 x 10 m. arranged  
in a square 50 x 50 m., oak woods, Cold Spring Harbor.

Tree reproduction under 1 in d.b.h. (12 species)

<i>Castanea dentata</i> (sprouts) -----	52%	frequency, class C, 8%
<i>Quercus velutina</i> -----	32	
<i>Prunus serotina</i> -----	32	
<i>Betula lenta</i> -----	32	
<i>Quercus montana</i> -----	24	class B, 58%
<i>Hicoria glabra</i> -----	24	
<i>Sassafras variifolium</i> -----	24	
<i>Hicoria alba</i> -----	28	
<i>Cornus florida</i> -----	16	
<i>Acer rubrum</i> -----	12	class A, 33%
<i>Quercus alba</i> -----	4	
<i>Nyssa sylvatica</i> -----	4	
Shrubs and Vines (10 species)		
<i>Kalmia latifolia</i> -----	96%	frequency, class E, 10%
<i>Viburnum acerifolium</i> -----	72	
<i>Vaccinium vacillans</i> -----	64	
<i>Azalea nudiflora</i> -----	64	class D, 30%
<i>Rubus hispidus</i> -----	24	
<i>Gaylussacia baccata</i> -----	24	class B, 20%
<i>Vitis Labrusca</i> -----	12	
<i>V. aestivalis</i> -----	12	

<i>Vaccinium vicinum</i> -----	8	class A, 40%
<i>Toxicodendron Toxicodendron</i> -----	4	
Herbs (16 species)		
<i>Unifolium canadense</i> -----	92%	frequency, class E, 6%
<i>Chimophila maculata</i> -----	44	
<i>Lysimachia quadrifolia</i> -----	44	class C, 13%
<i>Panicum Ashei</i> -----	32	
<i>Mitchella repens</i> -----	32	
<i>Aster divaricatus</i> -----	28	class B, 25%
<i>Juncoides campestre</i> -----	24	
<i>Peramium pubescens</i> -----	16	
<i>Monotropa uniflora</i> -----	12	
<i>Hypopitys americana</i> -----	12	
<i>Lespedeza repens</i> -----	8	
<i>Fragaria virginiana</i> -----	8	class A, 66%
<i>Potentilla</i> sp? -----	8	
<i>Fissipes acaulis</i> -----	8	
<i>Hieracium paniculatum</i> -----	4	
<i>Vagnera stellata</i> -----	4	
Total flora: A, 45%; B, 34%; C, 8%; D, 8%; E, 5%.		

TABLE 7

The biological spectrum of a small oak woods, Cold Spring Harbor.

	Raunkiaer's Normal, 1916	First Lake Woods	No. of Species
EP S Succulents -----	2	0	
E Epiphytes -----	3	0	
MM Mega-, Mesophanerophytes	8 } 46	15.2	14
M Microphanerophytes -----	18	9.8	9
N Nanophanerophytes -----	15	9.8	9
Ch Chamaephytes <sup>2</sup> -----	9	10.9	10
Hy H Hemicryptophytes -----	26	32.6	30
G Geophytes -----	4 } 32	18.5	17
HH Hydro-, Helophytes -----	2	0	
Th Therophytes -----	13	1.1	1
Saprophytes <sup>1</sup> -----		2.1	2
	100%	100%	92
EP: Epigeal life-form groups.			
Hy: Hypogeal life-form groups.			

<sup>1</sup> The two saprophytes should be thrown with the geophytes.<sup>2</sup> There are 34 species of bryochamaephytes not included in the spectrum bringing the total flora considered in the study to 126 species. No attention was given to algae, fungi and lichens, which, however, are relatively unimportant in the phytocoenosis.

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## Revision of the Western Primulas

Louis O. Williams

In attempting to determine a specimen of *Primula* from Utah, which was received in a collection, it became apparent that a careful study of the related species was necessary. The study has been extended to include all of the species known to occur from the Rocky Mountains to the Pacific, south of Canada and north of Mexico.

A short description of each entity, its synonyms, distribution and specimens examined are given. In a few instances so many specimens were seen that it was thought best to cite only a limited number of them.

Professor M. L. Fernald's\* treatment of the American representatives of the section *Farinosae* of *Primula* has been freely drawn from for species of that section occurring in the range of this revision.

Thanks are due the curators of several herbaria for the loan of material and the privilege of seeing material in the several herbaria visited. These, with the symbol designating the specimens from the respective herbaria, are: P. A. Munz, Pomona (P); Aven Nelson, Rocky Mountain Herbarium (Ry); Bassett Maguire, Utah State Agricultural College (Utah); J. M. Greenman, Herbarium of the Missouri Botanical Garden (M); Theodor Just, Herbarium Greeneanum at the University of Notre Dame (ND); George E. Osterhout, his personal herbarium (O); T. J. Fitzpatrick, Herbarium of the University of Nebraska (N); F. W. Gates, Herbarium of Kansas State College (K); B. F. Harrison, Herbarium of Brigham Young University (BYU); Paul C. Standley, Herbarium of the Field Museum of Natural History (F); O. J. Murie, his personal herbarium (Murie). Especial thanks are due Dr. J. M. Greenman for help freely given during the course of this study and for obtaining material from other herbaria.

### KEY TO THE SPECIES AND VARIETY

Bracts of the involucre gibbous at the base; lobes of the corolla deeply emarginate; limb of the corolla 1 cm. or less broad.

Calyx lobes acuminate to subulate-tipped; leaves mostly 6-12 cm. long.

Mature calyx-lobes usually exceeding the capsules; plants of s.e. Utah.

-----1. *P. specuicola*

Mature calyx-lobes exceeded by the capsules; plants from the Grand Canyon, Arizona

-----2. *P. Hunnewellii*

Calyx lobes acute to obtuse; leaves mostly less than 6 cm. long. -----3. *P. incana*

Bracts of the involucre not gibbous at the base; lobes of the corolla not deeply emarginate; limb of the corolla 1 cm. or more broad.

Apex of leaves subtruncate and dentate; Californian. -----9. *P. suffrutescens*

\* *Rhodora* 30:59-77, 85-104. 1928.

Apex of leaves not subtruncate, not dentate; not Californian.

Plants usually 1 dm. or more tall; inflorescence 3-20-flowered, umbellate.

Calyx farinose; corolla-tube in anthesis twice as long as the calyx.

Calyx in anthesis 4-5 mm. long, in fruit 5-7 mm. long; mature capsule 4-6 mm. long. -----4. *P. Rusbyi*

Calyx in anthesis 6-10 mm. long, in fruit 8-12 mm. long; mature capsule 7-9 mm. long. -----4a. var. *Ellisiae*

Calyx efarinose; corolla-tube equalling or only slightly exceeding the calyx. -----5. *P. Parryi*

Plants 1 dm. or less tall; inflorescence 1-3-flowered, not umbellate.

Involucral bracts 1-4 mm. long, subulate, inconspicuous; plants 1-4 cm. tall; 1-rarely 2-flowered. -----6. *P. angustifolia*

Involucral bracts 4-7 mm. long, not subulate, conspicuous; plant 5-10 cm. tall; usually more than 1-flowered.

Leaves lanceolate to oblong-lanceolate, acute or obtuse, widest near the middle, comparatively thick; capsule ovoid; stylopodium absent or poorly developed in anthesis. --7. *P. Cusickiana*

Leaves spatulate, rounded at apex; broadest above the middle, comparatively thin; capsule cylindrical; stylopodium well developed in anthesis. -----8. *P. Maguirei*

1. *PRIMULA SPECUICOLA* Rydb., Bull. Torr. Bot. Club 40: 461. 1913.

Leaves spatulate, narrowed to the subpetiolar base, membranaceous, sinuate-dentate, 4-13 cm. long, 0.7-2 cm. broad, farinose to efarinose below; scape 1-1.6 dm. tall; involucral bracts 4-10 mm. long, lance-attenuate, dorsally thickened but slightly gibbous at the base; yellowish corolla-tube 8-10 mm. long, its violet limb 6-10 mm. broad; capsule usually overtopped by the calyx-lobes.

Southeastern Utah, canyons and bluffs.

UTAH: Bluff City, July 12, 1895, *Eastwood 68* (M); Bluff, May 28, 1919, *Jones* (P); Moab, June 7, 1913, *Jones* (P, F); damp sandy soil under overhanging cliff, Cottonwood Canyon, Bluff, San Juan Co., June 26, 1932, *Maguire, Richards, Maguire & Hammond 5122* (Utah, M); damp sandy bank of Horse Heaven Canyon, Cottonwood Canyon, Bluff, San Juan Co., July 2, 1933, *Maguire et al. 5133* (Utah, M); moist shady cliff, very established soil, July 2, 1927, *Cottam 2540* (BYU).

2. *PRIMULA HUNNEWELLII* Fernald, *Rhodora* 36: 117. 1934.

Leaves spatulate, membranaceous, more or less farinose below, 4-9 cm. long, 0.7-1.5 cm. broad, sinuate-dentate; scape 5.5-11.5 cm. high; involucral bracts linear-subulate, 2-4 mm. long, dilated or gibbous at the base; capsule overtopping the calyx. (Compiled. See plate 282 in *Rhodora* 36, opposite page 132, 1934.)

No material of this has been seen. The plate and Professor Fernald's statement show that it is closely related to *P. specuicola*. The outstanding characters given to separate the species from *P. specuicola* are a capsule overtopping the calyx and shorter calyx. Whether or not the characters are of



specific value remains to be seen when abundant material is available. Miss Eastwood's number 68 has capsules which are both longer and shorter than the calyx.

3. *PRIMULA INCANA* Jones, Proc. Cal. Acad. Ser. 2. 5: 706. 1895.

*P. americana* Rydb., Bull. Torr. Bot. Club 28: 500. 1901.

*P. farinosa* subsp. *cufarinosa* var. *genuina* Pax, in Engler's Bot. Jahrb. 10: 199. 1905, in part.

*P. farinosa* var. *incana* Fernald, Rhodora 9:16. 1907.

Leaves oblong-ovate to spatulate, farinose beneath, shallowly denticulate, 1.5-8 cm. long, 0.5-2 cm. broad; scape 0.5-4.5 dm. high, strict; involucre bracts linear to linear-oblong, flat, broadly gibbous at the base; corolla-tube slightly exceeding the calyx (in one specimen seen much exceeding it); the limb 6-10 mm. broad, lilac; capsule only slightly exceeding the calyx.

Meadows, bogs and damp places, Mackenzie to Colorado and Utah. A few specimens from among many are cited.

MONTANA: moist meadows, Armstead, Beaverhead Co., June 20, 1920, *Payson & Payson 1735* (M, Ry); wet ground, mountain canyons, Deerlodge Co., *Blankenship 727* (M, P, N, F); Shite Sulphur Springs, Aug. 1893, *Startz* (M). WYOMING: sunny meadows, Rock River, June 30, 1913, *Macbride 2396* (M, Ry); Little Laramie River, *Nelson 3211* (P, F, K) and *1961* (M, Ry); Ft. Bridger, June 18, 1898, *Nelson* (Ry); low meadows, north Pilot Butte, July 1, 1901, *Merrill & Wilcox 749* (Ry); wet soil, Adam's Ranch, Jackson Hole, July 14, 1901, *Merrill & Wilcox 990* (Ry); damp soil, Hot Spring Bar, 20 mi. south of Jackson, July 19, 1901, *Merrill & Wilcox 1039* (Ry); Big Piney, June 11, 1931, *Murie 133* (Ry, Murie); Bernt Fork, Uinta Mts., July 30, 1935, *Cottam 6143* (F); in a bog at Red Buttes, July 6, 1896, *Greene* (ND). COLORADO: Wet Mt. Valley, 1873, *Brandeggee 378* (M); Gunnison, July 7, 1901, *Baker 361* (M, P, O, Ry); Leadville, *Schedin & Schedin* (Ry); wet meadow, West Cliff, June 24, 1917, *Johnston & Hedgcock 859* (Ry); Walden, 16 mi. mt. road to Steamboat Springs, Aug. 1, 1917, *Johnston & Hedgcock 300* (Ry); Sapinero, June 20, 1898, *Wheeler 539* (Ry). UTAH: meadows above Tropic, Clay, Alt. 7000, June 28, 1894, *Jones 5312av* (P, TYPE).

4. *PRIMULA RUSBYI* Greene, Bull. Torr. Bot. Club 8: 122. 1881.

*P. serra* Small, Bull. Torr. Bot. Club 25: 319. 1898.

Leaves spatulate, obtuse, 1.5-4 cm. broad, 3-12 cm. long, entire or crenate with small calloused teeth, efarinose, glabrous to short glandular pubescent; scape 8-20 cm. high, erect or ascending; involucre bracts 2-4 mm. long, lanceolate-subulate, plain or falcate; corolla tube 9-10 mm. long; limb 1.3-2 cm. broad, purple; calyx in anthesis 4-5 mm. long, in fruit 5-7 mm. long, lobes 2-2.5 mm. long, acute or acuminate, farinose; capsule 4-6 mm. long.

Damp shaded hillsides and ledges. Southwestern New Mexico and southwestern Arizona.

NEW MEXICO: Mogollon Mountains, Aug. 5, 1903, *Metcalf 399* (M, Ry); shaded hillsides, Mogollon Mountains, Aug. 1, 1881, *Rusby 252* (M). ARIZONA: Cave Creek Canyon, Chiricahua Mountains, July 25-Aug. 9, 1927, *Kusche* (P);

n. side of cliff, Barfoot Peak, Chiricahua Mountains, June 25, 1907, *Blumer*, 1539 (M, N, K, O); shade of rocks, Saucer Peak, Rincon Mountains, July 23, 1909, *Blumer* 3290 (M, N, F, ND); damp ledges, Santa Rita Mountains, July 25, 1885, *Pringle* (M, F, ND); moist rock crevices, Rustler's Park, Chiricahua Mountains, June 18-19, 1930, *Goodman & Hitchcock* 1179 (M, F); rocky summits, Carr Peak, Huachua Mts., July 16, 1909, *Goodding* 214 (Ry).

4a. *Primula Rusbyi* var. *Ellisiae* (Pollard & Cockrell) comb. nov.

*P. Ellisiae* Pollard & Cockrell, Proc. Biol. Soc. Wash. 15: 178. 1902.

Leaves oblanceolate to spatulate, obtuse or acute, 6-15 cm. long, 1-2 cm. broad, crenulate with small calloused teeth, efarinose; scape 11-20 cm. high, strict or ascending; involucre bracts 2-5 mm. long, linear to lanceolate-subulate, plain or falcate; corolla-tube 9-12 mm. long; corolla-limb 1.6-2.5 cm. broad, purple, often with a yellow eye; calyx in anthesis 6-10 mm. long, in fruit 8-12 mm. long, lobes 2-4 mm. long, acute or acuminate; capsule 7-9 mm. long.

Moist crevices and ledges. Central, west central and north central New Mexico.

NEW MEXICO: in crevices of cliffs, "only place known," alt. 10,300 ft., Sandia Mountains, June-July, 1911, *Ellis* 180 (M); top of Hillsboro Peak, Mimbres Mountains, Aug. 3, 1903, *Jones* 455 (P); White Mountains, Aug. 1, 1901, *Wootton* (M, P, F, K, Ry); rock ledges, alt. 10,500 ft., Sandia Rim, June 29, 1930, *Casteller* (Ry); Sawyer's Peak, Black Range, July 7, 1904, *Metcalf* 1081 (M, P, F); Sandia Mountains, *Arsene & Benedict* 16591 (F); Water Canyon, Magdalena Mountains, Socorro Co., July-August, 1910, *Herrick & Herrick* 209 (F).

Similar to the species except for the greater length of the calyx-lobes and the larger size of the capsule. It is usually a stouter plant and the flowers are usually larger in size. Pax, *Pflanzr.* IV. 237: 129. 1905, reduced it to *P. Rusbyi* but probably did not see material of it.

5. *PRIMULA PARRYI* Gray, Am. Journ. Sci. 34: 257. 1862.

*P. mucronata* Greene, *Pittonia* 3: 251. 1897.

*P. mucronata* var. *arizonica* Greene, l.c. 252.

*P. Parryi* *brachyantha* Rydb., Mem. N. Y. Bot. Gard. 1: 302. 1900.

*P. Parryi* f. *mucronata* Ckll., *Torreya* 15: 204. 1915.

Leaves spatulate-oblong to narrowly oblanceolate, obtuse or acute, often obscurely puberulent, 6-30 cm. long, 1-6 cm. broad, efarinose; scape 8-40 cm. high, erect; involucre bracts 3-12 mm. long; limb 1.5-3 cm. broad, deep red or purple in drying; calyx 7-15 mm. long, lobes 5-8 mm. long, lanceolate-acuminate, as long as the calyx-tube, glandular, usually purple, efarinose; capsule 7-11 mm. long, ovoid.

Moist alpine and subalpine meadows, forests, and cliffs. Montana to New Mexico, Nevada and Arizona along the high mountains. A few specimens from many are cited.

MONTANA: Trapper Peak, Bitter Root Mountains, August 31, 1921, *Kirkwood* 1245 (M); near Anaconda, Mt. Haggin, July 20, 1905, *Jones* (P); Darby, July 30, 1909, *Jones* (P). WYOMING: Ten Sleep Lakes, Big Horn Co., July 31, 1901, *Goodding* 446 (M, P, N); north side of Grand Teton, Teton National Park, July 19, 1932, *Williams* 897 (M, Ry); Surveyor Peak, Fremont Lake, Sublette Co., July 28, 1922, *Payson & Payson* 2828 (M, P, F, Ry); Medicine Bow Mountains, Albany Co., August 2, 1900, *Nelson* 7915 (M, P, N, Ry); eastern slope of Big Horn Mts., headwaters of Clear Creek and Crazy Woman River, July 20-August 15, 1900, *Tweedy* 3488 (Ry); Crazy Woman Creek, August 8, 1892, *Buffum* (ND). COLORADO: borders of alpine stream near the snow line, Middle Park, July, 1861, *Parry* 311 (M); Rocky Mountains, 1862, *Hall & Harbour* 379 (M, F); Mammoth Gulch, Tolland, *Munz* 3030 (P); Slide Rock Canyon, southern Colo., June 30, 1898, *Baker, Earle & Tracy* 238 (M, P, N, O); Argentine Pass, July 11, 1878, *Jones* 423 (P, ND); Little Ouray, Sept. 3, 1896, *Greene* (ND); Cameron Pass, 10,000 ft. July 15, 1896, *Baker* (ND). NEW MEXICO: Truchas Peak, August 8, 1908, *Standley* 4271 (M); Pecos Baldy, July 11, 1908, *Standley* 4271 (M). UTAH: La Motte Peak, Uinta Mountains, July 21, 1926, *Payson & Payson* 5003 (M, P, Ry); n. slope, Abajo Mountains, July 1-2, 1930, *Goodman & Hitchcock* 1379 (M, F); Fish Lake, August 10, 1894, *Jones* 5809 (M, P); American Fork Canyon, July 31, 1880, *Jones* 1393 (P, F); Silver Lake, Big Cottonwood Canyon, Sept. 30, 1909, *Jones* (P); Fish Lake, Uinta Mts., July 17, 1902, *Goodding* 1391 (Ry); Abajo Mts., August 17, 1911, *Rydberg & Garrett* 9711 (Ry); Mts. s. e. of Silver Lake, Big Cottonwood Creek, July 1, 1905, *Rydberg & Garrett* (Ry); American Fork Canyon, July 29, 1885, *Leonard* (K). NEVADA: East Humboldt Mountains, August 13, 1897 and July 27, 1900, *Jones* (P); Clover Mountain Range near Deeth, Elko Co., July 29, 1908, *Heller* 9214 (M); above timberline, n. slope Mt. Jeff Davis, August 26, 1933, *Maguire & Richards* 2732 (Utah); Ruby Mts., July 20, 1896, *Greene* [There are two sheets of this collection in the Greene Herbarium which are here designated as the type of *P. mucronata* Greene.] (ND). ARIZONA: San Francisco Peak, August 30, 1884, *Jones* 406 (P); Mt. Humphreys, July 28, 1883, *Rusby* 716 (M, F); San Francisco Mountains, June 30, 1923, *Hansen & Hansen* A613 (M, N); Mt. San Francisco, July 1889, *Greene* [Two sheets in the Greene Herbarium are here designated as the type of *P. mucronata* Greene var. *arizonica* Greene.] (ND); San Francisco Mountain at 11,000 ft. July 12, 1910, *Hill* [Cotype *P. mucronata* Greene var. *arizonica* Greene] (ND); below snow, Thomas Peak, White Mts., July 15, 1910, *Goodding* 604 (Ry); alpine stream, Thomas Peak, July 8, 1912, *Goodding* 1142 (Ry); Humphreys Peak of San Francisco Mountain, at 9-12,000 ft., August 7-10, 1898, *Macdougal* 407 (F).

This is the prettiest of the Rocky Mountain primulas and probably the largest native *Primula* in the United States. Occurring along moist cliffs and cold stream banks in the alpine and subalpine zones. It is the most common Rocky Mountain species. Nelson, Man. Ry. Mt. Bot. 373, 1909, says it is "A handsome plant but very rank smelling." The author has found it many times but has been unable to find a "rank smelling" specimen, on the contrary the slight odor that it does have is rather pleasing. A note on the type collection states that "the root is quite fragrant." The species is quite polymorphic, not only in the size of the plant and shape of the leaves but also in the size of the flowers, even on the same plant, generally the first flower to develop is much larger than the rest and may be twice as large as the last to develop.

6. *PRIMULA ANGUSTIFOLIA* Torr., Ann. Lyc. N.Y. 1: 34., pl. 3, fig. 3. 1824.  
*P. angustifolia* Helenae Pollard & Cockrell, Proc. Biol. Soc. Wash. 15: 79. 1902.

Leaves lanceolate-spatulate to linear-lanceolate, obtuse, entire, 1.5-5 cm.

long, 2-7 mm. broad, efarinose; scape 0.5-7 cm. tall; involucre bract 1-7 mm. long, occasionally 2 present, lanceolate, falcate; corolla-tube 5-8 mm. long; limb 1-2 cm. broad, purple or occasionally white; calyx 5-7 mm. long, lobes 2-3 mm. long, acute or acuminate, efarinose; capsule ovoid, 3-5 mm. long.

Rocky alpine summits and meadows, mountains of Colorado to n. New Mexico. The following specimens are selected from many.

COLORADO: Marshall Pass, July 19, 1901, *Baker* 498 (M, P, Ry); summit Pike's Peak, June 24, 1912, *Churchill* (M); Georgetown, June 28, 1878, *Jones* 333 (Utah, P); alpine meadows near Estes Park, June 21, 1929, *Mathias* 418 (M); mountains of Estes Park, July 22, 1903, *Osterhout* 2845 (O, P); rocky ground near top Mt. Corona, Gilpin Co., June 24, 1926, *Palmer* 31,307 (M); in granite land on the highest points of the Snowy Range, Middle Park, June 6, 1861, *Parry* 279 (M); West Spanish Peak, Alt. 2800-3000 m., July 6, 1900, *Rydberg & Vreeland* 5762 (Ry); Berthoud Pass, near Georgetown, Alt. 1200, August 16, 1884, *Sheldon* 270 (ND); Little Ouray Mt., Sept. 3, 1896, *Greene* (ND). NEW MEXICO: Pecos River, July 4, 1898, *Coghill* 40 (M, not characteristic); without exact locality, Sept., 1867, *Parry* 143 (M); vicinity of Santa Fe, Lake Peak, August 12, 1926, *Arsene & Benedict* 16145 (F); vicinity of Santa Fe, Lake Peak, July 15, 1926, *Arsene & Benedict* 15615 (F).

A small plant which usually bears but one flower on each scape, occasionally two, these vary as to size, if two are present they are generally smaller than when only one is present on specimens of a single collection.

#### 7. PRIMULA CUSICKIANA Gray, Syn. Fl. N. A. ed. 2. 21: 399. 1886.

*P. angustifolia* var. *Cusickiana* Gray, Syn. Fl. N. A. ed. 1. 21: 393. 1878.

*P. Brodheadae* Jones, *Zoe* 3: 306. 1893.

*P. Brodheadae* var. *minor* Jones, l. c.

*P. Parryi* according to Pax, *Pflanzr.* IV. 237: 128. 1905 as to syn. *P. Brodheadae* and locality.

Leaves lanceolate to oblong-lanceolate, 2-5 cm. long, 4-8 mm. broad, efarinose; scape 3-9 cm. tall; involucre bracts 3-10 mm. long, lanceolate, acute to subulate, falcate; corolla-tube 7-9 mm. long; limb 9-14 mm. broad, purple when dry; calyx 5-9 mm. long, obtuse to subulate, farinose to efarinose; capsule ovoid, 4-6 mm. long.

Moist meadows, eastern Oregon and adjacent Idaho.

OREGON: heavy soil, alt. 4000 ft., early spring, 1881, *Cusick* 360 (F); stony swales, eastern Oregon, April 13, 1898, *Cusick* 1832 (P, M, ND). IDAHO: Ketchum, May-June 1892, *Brodhead* (P, Type of *P. Brodheadae*); Bayhorse, July 1, 1892, *Brodhead* (P); east of Boise, in 1883, *Cleburne* (P); Boise City, Feb. and March, 1886, *Salt* (F); near Boise, in 1916, *Gageby* (Ry); Boise, May 10, 1910, *Sawyer* (Ry); Boise, March 3, 1908, *Miles* (Ry).

Pax, l. c., reduced to *P. Brodheadae* to *P. Parryi* without question but from citation of specimens he apparently did not see material of the former. Perhaps it was placed here because of Jones' allusion to *P. Parryi* in his description and also in that of var. *minor* (which Pax failed to account for), that the latter might be a variety of *P. Parryi*.

8. *Primula Maguirei* sp. nov.

Folia late spatulata, integra vel undulata, ad apicem rotundata; caulibus 4-10 cm. longis, gracilibus, 1-3-floris; bracteis involucri plerumque 2, lanceolatis aut lanceolato-subulatis; tubo corollae 9-11 mm. longo, limbo 14-25 mm. lato, lobis obovatis, emarginatis; filamentis 0.5 mm. longis; calyce 5-6 mm. longo, lobis 2-3 mm. longis, lanceolatis, obtusis vel acutis; capsula cylindrica usque ad 5 mm. longa.

Leaves broadly spatulate, attenuated into a winged petiole, entire or slightly undulate, rounded at the apex, 3-7 cm. long (mostly 5-6 cm. long) 8-12 mm. broad; scape 4-10 cm. long, slender, 0.7 mm. thick, bearing one to three flowers; involucre bracts usually two, the larger one 4-7 mm. long, lanceolate to lanceolate-subulate, the smaller 1-3 mm. long or vestigial, flat or falcate; corolla-tube 9-11 mm. long, about twice as long as the calyx; limb 14-25 mm. broad, lobes 6-10 mm. long, 4-5 mm. broad, obovate, emarginate, red or purple when dry; anthers 1.7 mm. long; filaments 0.5 mm. long; calyx 5-6 mm. long (to 9 mm. in fruit), the lobes 2-3 mm. long, lanceolate, obtuse or acute, farinose on both surfaces, not densely so; capsule cylindrical, 5 mm. long; stylopodium well developed and conspicuous on immature capsule; seed unknown. Fig. 1.

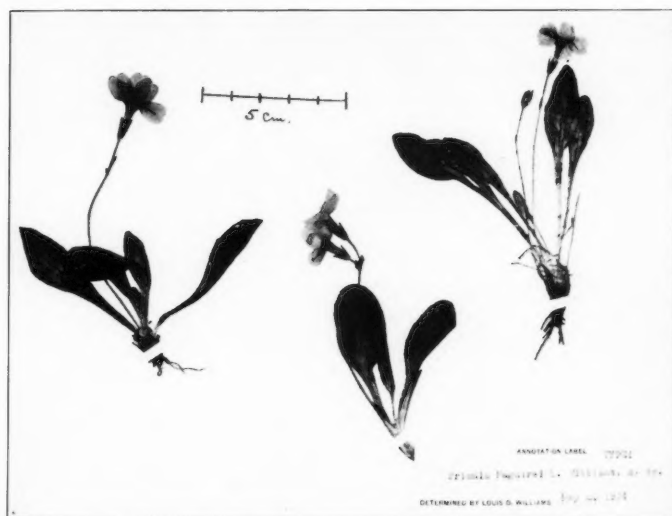


Fig. 1. Part of type specimen, *Maguire & Maguire 3650*, in Herb. Mo. Bot. Gard. x2/5.

Wasatch Mountains of northeastern Utah.

UTAH: damp overhanging rocks, ledges and cracks, east exposure, 5 miles up Logan Canyon, Cache Co. Elev. 5500 ft., April 19, 1932, *Maguire & Maguire 3650* (M. Type, Utah); rocky slope, north exposure, 1 mile up Logan Canyon, Cache Co.

Elev. 4800 ft., May 6, 1932, *Gerber 3650a* (Utah); n. exposure, Logan Canyon, Cache Co., Elev. 4400 ft., May 16, 1932, *Burke 3651* (Utah); under damp cliffs, lateral draw 4 miles up Logan Canyon, Cache Co., May 28, 1933, *Muenschner & Maguire 2399* (Utah, M); cliffs, Logan Canyon, Cache Co., May 10, 1911, *Aldons & Owen* (Ry); moist crevices in cliffs 3 miles up Logan Canyon from the University, Cache Co., Elev. 5500 ft., May 27, 1935, *Williams 2149* (M, ND).

This species is most closely related to *P. Cusickiana*. It may be distinguished by the larger, spatulate comparatively thin leaves which are broadest above the middle; the corolla-tube is twice as long as the calyx in contrast to as long or less than twice as long in *P. Cusickiana*; in anthesis the well developed stylopodium in contrast to a poorly developed or absent one. The capsule is cylindrical not ovoid. Polymorphism is well illustrated in the flowers of this species. When only one flower is borne on each scape it is comparatively large, if two are borne they are as a rule both smaller than in the former case and the first to develop, which is on the side toward the larger bract, is larger than the second one which is opposite the smaller bract, in case three flowers develop the size is smaller in each successive one to appear and generally the corollas are smaller than in both the former cases.

9. *PRIMULA SUFFRUTESCENS* Gray, Proc. Am. Acad. 7: 371. 1868.

Leaves cuneate-spatulate, 3-8-toothed at the subtruncate apex or sharply serrate half the length, 1.5-3 cm. long, 4-12 mm. broad below the apex. efarinose; scape 3-13 cm. high, from a suffruticose base; involucre bracts 2-6 mm., lanceolate-subulate, flat or falcate; corolla-tube 5-8 mm. long; limb 14-22 mm. broad, red to purple; calyx 5-7 mm. long, lobes 2.5-4 mm. long, lanceolate to broadly lanceolate, acute, efarinose; capsule ovoid, 5-6 mm. long.

Rocky slopes and summits, high mountains of east central California. A few specimens from the many at hand are cited.

CALIFORNIA: Mt. Whitney, August 15, 1904, *Culbertson 4523* (P, M); Mt. Whitney, August 15, 1904, *Culbertson 4524* (ND, F, M, P); east slope of Mt. Anderson, Placer Co., August 1895, *Sonne* (M, P); Mt. Stanford, July 1886, *Sonne* (ND); mountain above cold stream, Placer Co., *Sonne 214* (ND, F); summit, Sierra Nevada Mountains, July 26, 1900, *Jones 6441* (M, P); Sept. 23, 1882, *Pringle* (F); Castle Peak, Nevada Co., August 5, 1903, *Heller 7096* (M, P, Ry); western base, Mt. Whitney, Tulare Co., *Bacigalupi 1748* (P); Sierra Valley, 1874, *Lemmon 145* (M); on Cloud's Rest, in 1872, *Gray* (M); Kaiser Peak, Fresno Co., July 19, 1918, *Grant 1147* (M, Ry).

## Morphology of the Gynobase in *Mertensia*

John Adam Moore

The conformation of the ring-like disc or gynobase surrounding the gynoecium varies greatly among the genera of *Boraginaceae*. The morphology of the gynobase has been taken for granted by most systematists, and has been used descriptively in connection with description of nutlet attachment. No morphological or evolutionary significance has been attached to the gynobase.

In other families, anatomical and morphological studies have demonstrated that many discs, nuptial nectaries, and floral squamellae may be interpreted in terms of the other appendages of the flower. For example, it is believed that the sheathing disc about the carpel in many *Leguminosae* represents an abortive set of stamens.<sup>1</sup> Structures adjacent to the gynoecium which have been observed in many *Apocynaceae* are interpreted as carpelodes.<sup>2</sup>

The heteromorphic nature of the gynobase of *Mertensia* is apparent on gross examination (Figs. 15, 16). The four unequal lobes of the gynobase alternate with the four nutlets of the pistil. Opposed to the carpels are two small obtusely triangular pointed lobes. Alternated with the carpels are the two large lobes which equal or surpass the nutlets in size. For a better understanding of the morphology of the gynobase it is necessary to describe briefly the anatomy of the flower in *Mertensia*.

The vascular anatomy of the flower is not especially complicated in *Mertensia*. In most respects the description given here applies to other members of the *Boraginaceae* which I have examined (Figs. 1-13). The pedicel contains a circle of ten strands, alternately large and small (Fig. 1). The five smaller traces swing outward and upward to supply the sepals (Fig. 4). These strands split radially into 3 parts after they leave the stele. Lateral strands of adjacent calyx lobes do not fuse. The sepal gaps close, and then the petal and stamen traces begin to depart (Fig. 5). Each stamen receives one trace. There are five petal traces, and these split radially into three members after leaving the stele.

The petal and stamen trace gaps close and the stele becomes provascular except for the strands which are to supply the carpels (Fig. 7). Each carpel is provided with three traces. The two ventrals of each carpel swing inward and upward toward the center of the flower, each eventually ascending through the placenta into the funiculus (Figs. 10-12). The dorsal bundle pursues a devious upward course which leads into the style. The median lateral bundles seen in the nutlet walls apparently arise from the placental bundles, curve upward into the wall of the nutlet and then gradually die out.

<sup>1</sup> Moore, J. A. The vascular anatomy of the flower in the papilionaceous *Leguminosae*. *Amer. Journ. Bot.* 23: in press. 1936.

<sup>2</sup> Woodson, R. E., Jr. Studies in the *Apocynaceae* I. *Ann. Mo. Bot. Gard.* 17:1-212. 1930.



It is the path of the carpel dorsal traces that sharply distinguishes *Mertensia* from the other genera of *Boraginaceae* which the writer has examined. In *Echium* sp., *Lithospermum canescens* (Michx.) Lehm., *Plagiobotrys cognatus* (Greene) Johnston, *Hackelia floribunda* (Lehm.) Johnston, *Myosotis* sp., and *Eritrichium elongatum* Wight, the carpel dorsals ascend vertically directly into the style. In every species of *Mertensia* which has been examined (*M. humilis* Rydb., *M. brevistyla* Wats., *M. maritima* (L.) S. F. Gray, *M. virginica* (L.) Link) the dorsal bundle of each carpel ascends upward unto a lobe of the gynobase, turns inward and downward, swings toward the style, and turns abruptly to pass into the style (Fig. 14). It is the smaller pair of gynobase lobes opposed to the carpels through which the bundles pass.

The remaining provascular stele loses its identity as it passes upward, and it is impossible to state definitely that the larger gynobase lobes have a vascular supply.

From the course of the dorsal bundles we may infer that the smaller "hunchback" members of the gynobase were formed from the carpels as a result of the infolding necessarily accompanying the reduction of the gynoeium to its present four-lobed form.

The homology of the larger lobes of the gynobase is somewhat more difficult to ascertain. It is possible that the larger lobes may have been derived from stamens. Most of the evidence is opposed to this interpretation. There are only two structures concerned and they alternate with the carpels. If this be a case of staminody one should expect five sterile structures rather than just two. Furthermore, any reduced series of five stamens could not possibly have two alternating with the pair of carpels.

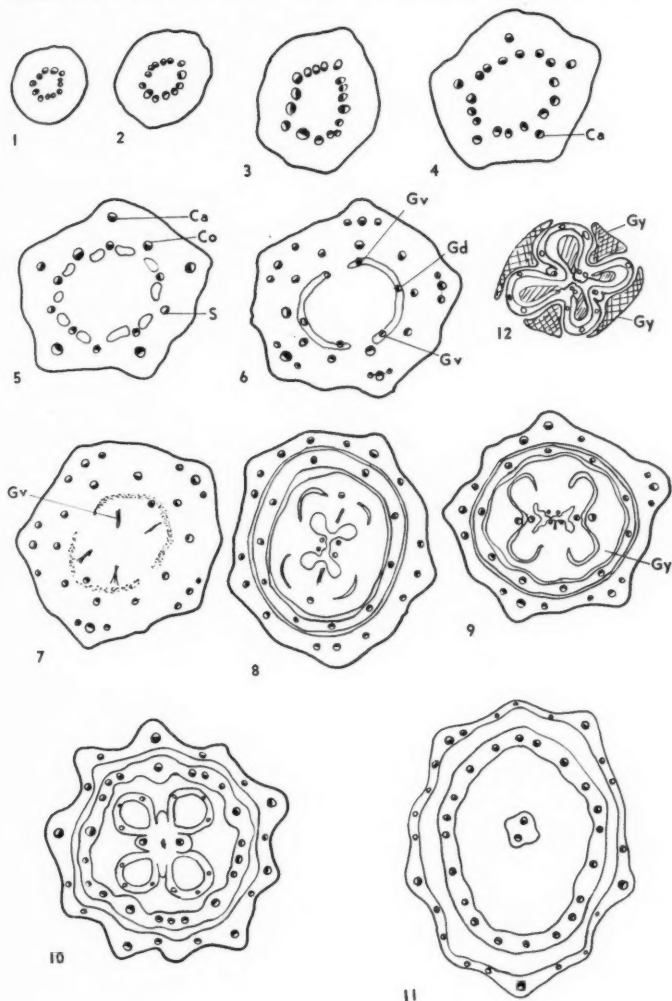
However, it seems more likely that the larger lobes may have been derived from carpels. In addition to the negative evidence given above, there is considerable positive evidence that we are dealing with carpellobes. The alternate arrangement is one which is possible for a pair of sterile carpels. In size these members approximate the nutlets in size at anthesis (a condition occurring in other families). Their gross morphology suggests carpel rather than stamen. The absence of mature vascular tissue in these structures militates against the acceptance of the carpellobes interpretation, but the writer's own observations on carpellobes in other families indicate that since series passing from free, massive, vascularized carpellobes to fused non-vascularized carpellobes may occur in the same family, the absence of vascular tissue should not bar this interpretation.

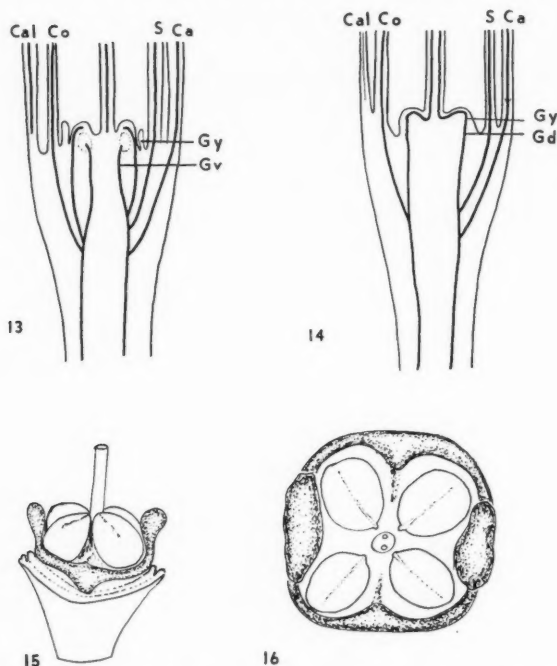
The occurrence of carpellobes in various stages of reduction may be seen in a number of families of *Sympetaleae*. In the *Apocynaceae* especially clear series may be observed, while in the *Gentianaceae*, the end members in a reduction series may be found in some forms.

The two smaller gynobase lobes opposed to the carpels are obviously just part of them. The large alternating members of the gynobase complex seem

to be carpellobes, if we will take the evidence of vascular anatomy, external morphology, and comparative morphology.

For the serial microtome sections which were placed at my disposal I am indebted to Mr. Louis O. Williams of the Henry Shaw School of Botany.





Figures 1-8 and 11-16 from *Mertensia virginica*, the others from *M. brevistylis*.

Abbreviations used: Ca, calyx; Cal, calyx lateral; Co, corolla, petal; S, stamen; G, gynoeceum; Gd, carpel dorsal; Gv, carpel ventral; Gy, gynobase.

1. Pedicel. 2. Beginning of calyx trace departure. 3. Later stage in calyx trace departure. 4. Calyx traces free from stele. 5. Petal and stamen traces departing simultaneously. 6. Calyx laterals split off. Six carpel strands apparent in provascular ring. 7. Provascular ring still evident. Carpel ventrals passing to center. 8. Calyx and corolla tubes separate from gynoeceum complex. Lower portion of gynobase shown. Note position of carpel dorsal as it passes up and swings inward into styler position. Placental bundles are in place. 9. Higher level, not traces with opposed phloem in gynobase and stele. 10. At a level above gynobase, the placental strands have passed into the ovules. Medial lateral traces may be seen in the nutlet walls. Styler bundles normally orientated. Petal traces split radially into 3 parts. 11. Section of flower through style. Note numerous calyx laterals. 12. Gynoeceum at placental level showing appearance of gynobase lobes in section. 13. Diagram of path of traces in plane of carpel ventrals. 14. Diagram of path of traces in plane of carpel dorsals. 15. Lateral view of gynobase smaller lobes opposed to carpels, larger alternating. 16. Gynobase (shaded) and pistil seen from above.

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## The Hemiptera of Indiana, I. Family Gerridae

Howard O. Deay and George E. Gould

The species of water striders,—known also as water spiders, pondskaters and wherry-men—inhabit the ponds, small lakes, creeks and quieter waters of the larger streams in Indiana. Being gregarious, they often congregate in great numbers in inlets, in the slack waters below boulders, or in the swift current itself. Ordinarily, they are predacious and feed upon such aquatic insects as the larvae of midges and nymphs of back-swimmers, or upon such terrestrial insects as may fall into the water. Besides living insects, they devour also insects that have been dead for some time, and, when food is scarce, they even practice cannibalism eating their own nymphs and the weaker adults.

The writers have personally collected most of the material described in this paper. Their specimens, now deposited in the Purdue Entomological Collection, come from every section of the State and from nearly every county.

Since most species include wingless, short-winged and long-winged forms, an attempt has been made to use characters in the keys which will apply to all three forms. Specific keys are made for both sexes although the females of some species of *Gerris*, as noted in the key, are so similar in appearance that it is very difficult to find clear-cut diagnostic characters.

Seventeen species and one variety of Gerridae, representing two subfamilies and five genera, are known to occur in the state. Since two other species, *Gerris conformis* (Uhler) and *G. incurvatus* Drake and Hottes, may possibly occur here, description of them are included. Blatchley in his "Heteroptera of Eastern North America" records nine species of the family as occurring in Indiana.

### Systematic Position

The *Gerridae* belong to the superfamily *Gerroidea*, one of the semi-aquatic groups of Hemiptera. They may be distinguished from all other Hemiptera by the facts that the last segment of the tarsi are more or less split, and that the tarsal-claws, especially of the fore tarsi, are inserted before the apex of the last tarsal segment. The *Gerridae* may be distinguished from the *Velidae*, the other member of the superfamily, by the following key:

1. Hind femora extend much beyond apex of abdomen. Middle and hind pairs of legs much closer together at base than fore and middle legs ----- *Gerridae*
- 1'. Hind femora extend but little if any beyond apex of abdomen. Middle legs, except in the genus *Rhagovelia*, equidistant from the fore and hind legs. -- *Velidae*.

## Family GERRIDAE Amyot and Serville, 1843

Usually narrow bodied, elongated, long-legged insects. Head horizontal, shorter than pro- and mesonota united. Antennae filiform, 4-segmented. Rostrum 4-segmented, segments I and II very short. Undersurface of body, sometimes whole body, clothed with short, close-set pile. Wings usually absent, but wingless, brachypterous and macropterous forms may occur within the same species; wings when present not divided into distinct clavus and membrane. Fore legs short, raptorial. Middle and hind legs long, slender, hind femora much surpassing apex of abdomen. Front coxae distant from middle pair, the middle and hind coxae close together. Tarsi 2-segmented, terminal segment bifid at apex. Tarsal claws inserted before apex.

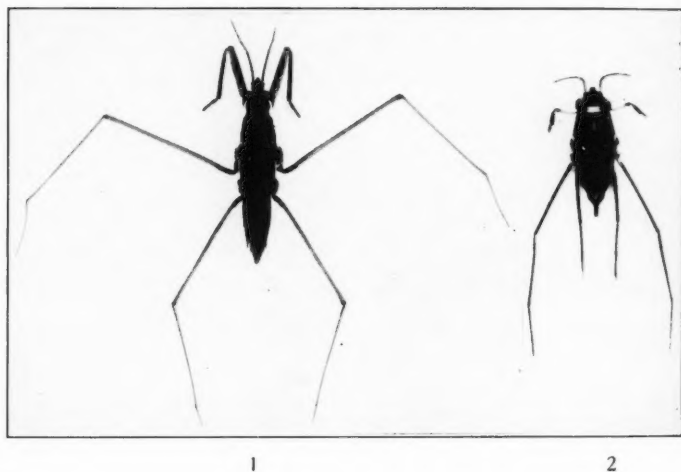


Fig. 1. *Gerris remigis*, male, actual length 14 mm. (2) *Rheumatobates rileyi* var. *palosi*, female, actual length 2.8 mm.

There are three subfamilies of Gerridae: (1) *Gerrinae*, (2) *Halobatinae*, and (3) *Ptilomerinae*. The third is restricted to central and southeastern Asia and adjacent islands, but representatives of the other two are found in Indiana.

## Key to the subfamilies of Gerrinae and Halobatinae

- 1. Inner margin of eyes concave or emarginate (notched). Body comparatively narrow and long; abdomen usually longer than thorax.....subfamily *Gerrinae*
- 1'. Inner margin of eyes convexly rounded, not emarginate. Body short and broad; abdomen usually very short .....subfamily *Halobatinae*

## Subfamily GERRINAE Bianchi, 1896

Medium to large sized water-striders, usually elongate and with sides of body sub-parallel. Generally black to brown in color, frequently marked with a silvery pubescence. Eyes concavely rounded on inner margins and emarginate. Thorax varies in form according to development of wings. Abdomen composed of six visible segments, and two genital segments.

Eleven species and two genera of this subfamily are known to occur in Indiana and two other species, *G. conformis* (Uhler) and *G. incurvatus* Drake and Hottes may possibly occur here.

## Key to the Genera of Indiana Gerrinae

1. Dorsal surface of head and pronotum glabrous, shiny. First segment of fore tarsus short, about half as long as second ..... *Limnogonus*
- 1'. Dorsal surface of head and pronotum sericeous, dull. First and second segments of fore tarsus subequal in length ..... *Gerris*

## I. Genus GERRIS Fabricius, 1794

Head short; eyes large, prominent, their inner margin concave or sinuate behind the middle. Antennae moderately long, rarely reaching beyond hind margin of pronotum, first segment longest. Beak short, reaching onto the mesosternum. Tarsal segments of front legs about equal in length. Pronotum dull, fused to mesonotum in wingless forms.

## Key to the Indiana Species of Gerris (males)

1. Last ventral abdominal segment simply rounded on posterior margin. (Figs. 6, 7, 13) ..... 2.
- 1'. Last ventral segment with a median notch on posterior margin (Figs. 4, 8-12) 5.
2. (1) Length 8 to 11 mm. .... *G. canaliculatus*.
- 2'. (1) Length 12 mm. or over ..... 3.
3. (2') Antennal segment I shorter than II and III united ..... *G. dissortis*.
- 3'. (2') Antennal segment I equal to or longer than segments II and III united. 4.
4. (3') Last ventral segment with prominent deep broad, depressed median furrow (Fig. 6) ..... *G. nebularis*.
- 4'. (3') Last ventral segment without a median furrow (Fig. 7) ..... *G. conformis*
5. (1') Large species, length 12 to 16 mm. (Fig. 1). .... *G. remigis*.
- 5'. (1') Small species, length less than 11 mm. .... 6.
6. (5') First genital segment beneath with tuft of long, conspicuous hairs on each side of median ridge (Fig. 10) ..... *G. comatus*.
- 6'. (5') First genital segment without tuft of long hairs ..... 7.
7. (6') Anterior side margins of pronotum with a dusky yellow or silvery stripe 8.
- 7'. (6') Side margins of pronotum without a stripe ..... 9.
8. (7) First genital segment as broad as long, the median notch on sixth ventral rectangular (Fig. 12) ..... *G. buenoi*.
- 8'. (7) First genital segment distinctly longer than wide, median notch rounded (Fig. 11) ..... *G. argenticollis*.
9. (7') Omphalium strongly produced, prominent ..... *G. alacris*.
- 9'. (7') Omphalium not prominent ..... 10.

10. (9') First genital segment strongly impressed on each side ..... 11.  
 10'. (9') First genital segment plump, scarcely impressed on each side of middle  
 (Fig. 8) ..... *G. insperatus*.  
 11. (10) Notch of sixth ventral broadly rounded ..... *G. incurvatus*.  
 11'. (10) Notch of sixth ventral narrowly rounded, somewhat U-shaped (Fig. 9)  
 ..... *G. marginatus*.

Key to Indiana Species of *Gerris* (female).

1. Large species, length 12 mm. or more ..... 2.  
 1'. Smaller species, length 11 mm. or less ..... 5.  
 2. (1) Antennal segment I equal to or longer than II and III united ..... 3.  
 2'. (1) Antennal segment I shorter than II and III united ..... *G. dissortis*.  
 3. (2) Antennal segment I more or less equal to segments II and III united ..... 4.  
 3'. (2) Antennal segment I distinctly longer than II and III united, II and III  
 of equal length ..... *G. conformis*.  
 4. (3) Connexival spines long, slender, curved in and upward, as long as genital  
 segments ..... *G. nebularis*.  
 4'. (3) Connexival spines short, as long as first genital segment (Fig. 3) ..... *G. remigis*.  
 5. (1') Anterior side margins of pronotum with a dusky yellow or silvery stripe ..... 6.  
 5'. (1') Anterior side margins without a stripe ..... 8.  
 6. (5) Anterior, lateral stripe reaching basal margin of pronotum ..... 7.  
 6'. (5) Anterior, lateral stripe not reaching basal margin of pronotum ..... *G. canaliculatus*.  
 7. (6) First genital segment as wide as long, with a median ridge basally and  
 strongly depressed on each side ..... *G. argenticollis*.  
 7'. (6) First genital segment flattened, without prominent ridge ..... *G. buenoi*.  
 8. (5') Connexival spines strongly incurved, their tips clothed with short stiff  
 hairs ..... 9.  
 8'. (5') Connexival spines not strongly incurved ..... 10.  
 9. (8) Antennal segment one-third longer than IV ..... *G. incurvatus*, 1  
 9'. (8) Antennal segment I a little longer than IV ..... *G. comatus*, 1  
 10. (8') Connexival spines moderately thick, reaching to apex of first genital  
 segment ..... *G. marginatus*, 1  
 10'. (8') Connexival spines thick, not reaching to apex of first genital segment ..... 11.  
 11. (10') Genital segments beneath and lateral margins of first above yellowish  
 ..... *G. insperatus*, 1  
 11'. (10') Genital segments dark ..... *G. alacris*, 1

1. *Gerris remigis* Say, 1832

Figs. 1, 3, 4.

Elongated, stout-bodied, forms usually brownish-black but occasionally reddish-brown; thickly clothed with silvery gray pubescence. Legs and antennae reddish-brown, somewhat lighter than body. Segment I (basal) of antennae nearly as long as II and III united, II and III of about equal length and both shorter than IV. Connexiva (edges of abdomen) extended back as spine-like processes not reaching the tip of genital segments. Last ventral abdominal segment of male deeply and roundly notched on its median pos-

1 The females of these species are so similar externally that it is difficult to separate them.

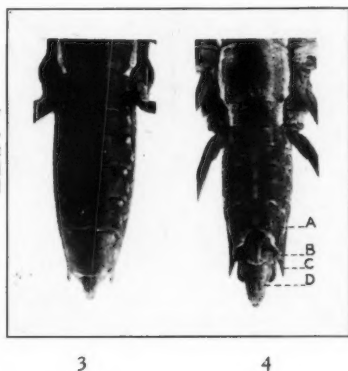


terior margin; first genital segment with median ridge very long, broad and prominent, depressed strongly on each side. Connexival spines of female much shorter than male, almost reaching tip of genital segments.

Length, 12-16 mm.; width, 3-4 mm.

This is the commonest and most widely distributed water-strider in Indiana. It occurs on most ponds and lakes and frequently is found in the quiet pools of the streams. Hibernation takes place along the banks under stones, logs and other debris. Schools of them are seen on the water in late fall and again in early spring when the edges of the pools are frozen. The

Fig. 3. *Gerris remigis*, ventral view female abdomen. (4) *Gerris remigis*, ventral view, male abdomen. A. Last abdominal segment. B. First genital segment. C. Connexival spine. D. Second genital segment.



apterous form is much more common, but often the winged forms are encountered on isolated ponds, temporary pools and water tanks.

There are specimens in the Purdue Collection from the following counties: Benton, Carroll, Clark, Decatur, DeKalb, Elkhart, Fountain, Greene, Hamilton, Harrison, Howard, Jefferson, Jennings, Johnson, Kosciusko, Lawrence, Miami, Marshall, Monroe, Morgan, Noble, Owen, Parke, Ripley, Starke, Tippecanoe, Warren, White and Whitley.

## 2. *Gerris nebularis* Drake & Hottes, 1925

Fig. 6.

Body elongated, moderately robust, color brownish-black. Wings often abbreviated. Antennal segments I equal in length to II and III united. Hind lobe of pronotum with distinct median carina. Sixth ventral segment of male broadly rounded and with a deep, broad median furrow; first genital segment with a high broad median ridge, strongly depressed on each side; connexival spines long, slightly diverging and reaching beyond the first genital segment. Connexival spines of female curved upward and inward, longer than the genital segments.

Length, 14-16 mm.; width, 2.3 mm.

This species, often confused with *G. remigis*, has a wide distribution in the United States. The only record from Indiana is a specimen from Kosciusko County, collected by G. E. Gould.

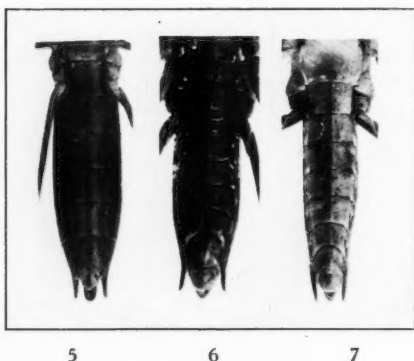


Fig. 5. *Gerris dissortis*, ventral view, female abdomen. (6) *Gerris nebularis*, ventral view, male abdomen. (7) *Gerris conformis*, ventral view, male abdomen.

### 3. *Gerris marginatus* Say, 1832

Figs. 9, 14.

Body elongated, moderately robust, black or brownish-black, usually with a pale powdery, longitudinal stripe on each side of pronotum; body and veins of wings with yellowish pubescence, which are whitish beneath. Antennae and legs reddish-brown, front femora darker. Antenna short; segment I about equal to II and III united, and scarcely longer than IV. Wings usually present and usually reaching to tip of abdomen. Venter of male with median carina, median notch on last ventral narrowly rounded; first genital segment with a median ridge, depressed on each side. Connexiva of female of uniform width or widening apically over last dorsal segment; connexival spines reaching to or surpassing apical margin of first genital segment.

Length, 8-11 mm.; width 2.2-2.5 mm.

With the exception of *G. remigis*, this is the commonest species of water-strider in the state. They are found on ponds and lakes and occasionally on running streams.

There are specimens in the Purdue collection from the following counties: Adams, Benton, Carroll, Clark, Clay, Elkhart, Fulton, Grant, Harrison, Howard, Jefferson, Knox, Kosciusko, Lake, Madison, Marshall, Miami, Montgomery, Morgan, Noble, Pulaski, Tippecanoe, Wabash, Warren, Wells, White and Whitley. The dates of collection extend from March 30 to October 8.

### 4. *Gerris comatus* Drake & Hottes, 1925

Fig. 10

Size, color, and general appearance similar to *G. marginatus*. Apterous, short- and long-winged forms often taken. Male with median notch on last

ventral segment narrowly rounded; first genital segment with a median ridge and tufts of long pale hairs in the depressed area on either side. Connexival spines of female strongly curved towards the median line and clothed with numerous bristly hairs.

Length, 7-9 mm.; width 2.5 mm.

This species is similar to and often confused with *G. marginatus*, from which it differs by having the first genital segment of male clothed with long hairs.

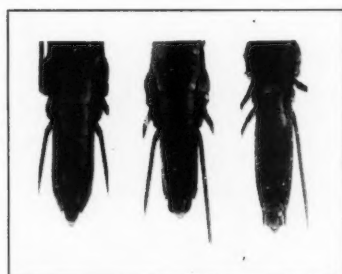


Fig. 8. *Gerris insperatus*, ventral view, male abdomen. (9) *Gerris marginatus*, male abdomen. (10) *Gerris comatus*, ventral view, male abdomen.

8

9

10

Specimens in the Purdue collection are from Elkhart, Kosciusko, Noble, Pulaski, Tippecanoe, and Warren counties. The dates of collection range from April 8 to August 26.

#### 5. *Gerris insperatus* Drake & Hottes, 1925

Fig. 8

Size, color and general appearance similar to *G. marginatus*. Only winged forms known. Venter of male with median carina becoming more noticeable on last two segments; median notch on last ventral somewhat more rounded than *marginatus*; first genital segment short, plump, very faintly impressed on each side, and without a distinct median ridge. Connexiva of female of last dorsal segment narrowing apically; connexival spines thick and short, scarcely reaching the apical margin of first genital segment.

Length, 7.4-8.6 mm.; width 2.3-2.5 mm.

This species is difficult to separate from *G. marginatus*.

Specimens collected from Morgan and Tippecanoe counties, dates April 13 and May 27.

#### 6. *Gerris incurvatus* Drake & Hottes, 1925

Body elongated, moderately robust; brownish-black. Antennal segment I slightly longer than II and III united, about one-third longer than IV. Last ventral segment of male with a deep, broadly rounded notch; first genital segment strongly depressed on each side, the median ridge broad at base.

Connexival spines of female curved strongly inward, their tips clothed with short stiff hairs.

Length, 7.6-8.7 mm.; width 2.3-2.5 mm.

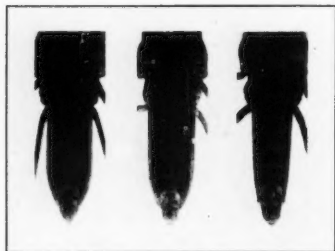
Drake & Harris (1934) assert that this species inhabits the Northwest, although they have examined specimens from Illinois. It has not been recorded from Indiana. It is very similar to *G. marginatus*, but the apical notch of the last ventral segment is "more rounded."

#### 7. *Gerris buenoi* Kirkaldy, 1911

Fig. 12

Body robust; brownish-black; legs lighter. Pronotum with median carina and a marginal line silvery or dull yellow. Winged, short-winged and apterous forms occur. Segment I of antennae equal in length to II and III united. Sixth ventral of male with the median notch broad and rectangular; first genital segment broad, its length at middle about equal to its width; connexival spines short, fitting against the first genital. Connexival spines of female short; first genital segment below broad and flattened.

Length, 7-8 mm.; width 1.3-1.6 mm.



11

12

13

Fig. 11. *Gerris argenticollis*, ventral view, male abdomen. (12) *Gerris buenoi*, ventral view, male abdomen. (13) *Gerris canaliculatus*, ventral view, male abdomen.

This species has a Northern range of distribution across the United States. Although not recorded from the State by Blatchley, the authors collected it from woodland pools in Kosciusko and Warren counties between the dates of April 15 and October 17.

#### 8. *Gerris argenticollis* Parshley, 1916

Fig. 11

Elongated; brownish-black forms. Pronotum with median and marginal stripes yellowish, the latter clothed with silvery pubescence. Antennal segments II and III about equal in length, united about as long as I and somewhat longer than IV. Wings whitish between the veins on the inner margin of the base; often abbreviated. Venter with a distinct median carina. Sixth ventral segment of female with a narrowly-rounded apical notch, the first genital segment distinctly longer than broad, narrowed posteriorly depressed on

each side of narrow median ridge. Connexival spines of female stout, as long as first genital segment; first genital as wide as long, with a median ridge toward the base, and strongly depressed on each side before the middle.

Length, 7.0-8.5 mm.; width 1.6-1.8 mm.

This species often occurs in company with the preceding species in woodland pools. Reported from the state by Drake and Harris (1934).

There are specimens in the Purdue collection from Benton, Clay, Kosciusko, Porter and Tippecanoe counties, collected between April 15 and August 9.

#### 9. *Gerris alacris* Hussey, 1921

Elongated; brownish-black insects; abdomen beneath usually in part dull yellow. Antennae brown, last two segments darker; segment I equal to II and III in length, one-fourth or more longer than IV. Wingless, short- and long-winged forms common. Omphalium on mesosternum of male strongly produced and prominent; sixth ventral with median notch broadly rounded, sides somewhat straight; first genital short, with a median ridge and slight depressions on each side. Connexival spines of female very short, not reaching to middle of first genital segment.

Length, 7-10 mm.; width 2.1-2.9 mm.

Blatchley (1926) records this species from Lake County.

#### 10. *Gerris dissortis* Drake & Harris, 1930

Fig. 5

Body elongated, sides parallel, color a dark reddish-brown; coxae, coxal cavities and prosternum yellow, the remainder of legs and antennae light brown; meso- and metasternum blackish; abdomen dull yellow with broken cross stripes of brown. Front lobe of pronotum with conspicuous black spots on each side of median line. Legs long and slender, extending beyond abdomen about length of body. Antennae at least half as long as body, segment I shorter than II and III united. Sixth ventral segment of male broadly rounded, without notch; connexival spines long, slender and acute, reaching but slightly beyond the apex of first genital segment; this segment without median ridge at base. Connexival spines of female equal in length to both genital segments.

Length, 12-14.5 mm.; width 1.6-2 mm.

This species has been called *G. rufoscutellatus* Latreille—a European form. Blatchley (1926) reports it under that name. One specimen in the Purdue collection was collected by G. E. Gould in a small, weedy woodland pool on October 8 in Tippecanoe County. It has been recorded from Indiana by Drake & Harris (1934).

#### 11. *Gerris canaliculatus* Say, 1832

Fig. 13

Body elongated, slender, sides parallel; color varying from dark reddish-

brown to brownish-black. Pronotum extending over mesonotum in wingless forms, a longitudinal carina down the median line in all forms, this carina fulvous on the front lobe; lateral pale stripe not quite reaching front margin. Antennae brownish, at least half as long as body; segment I usually shorter than II and III united. Legs brown, long and slender. Sixth ventral segment of male broadly rounded, without a notch; connexival spines long, slender, slightly diverging, reaching slightly beyond the apex of the first genital segment; this segment very broad, cylindrical, beneath with a short, low basal ridge, and constricted before the apex. Female with sixth ventral slightly produced at middle; connexival spines long, extending to or almost to apex of genital segments.

Length, 8-12 mm.; width 1-1.25 mm.

This species, previously unrecorded from the State, was collected in Tippecanoe and Carroll counties by G. E. Gould on April 22 and July 15 respectively. The Tippecanoe County specimens were taken in weeds along the edge of a running stream.

#### 12. *Gerris conformis* (Uhler, 1878)

Fig. 7

Elongated, brownish-black striders. Antennal segment I distinctly longer than II and III united, II and IV about equal in length. Legs long and slender. Venter dark, with small silvery spots on each side between segments. Connexival spines very long. Venter of male with a median, brownish line; broadly and roundly emarginate behind; first genital segment plump at base, strongly depressed on each side toward the apex, thus forming a median basal triangular ridge; connexival spines as long as genital segments. Connexival spines of female long.

Length, 15-16.5 mm.; width 2.7 mm.

This species is closely related to *G. nebularis* from which it differs in having longer first antennal segments and connexival spines.

It has not been recorded from Indiana, but has been taken in Michigan and Ohio.

#### II. Genus LIMNOGONUS Stal, 1868

Pronotum glabrous, shining, in wingless forms not fused with mesonotum. Antennae long and slender, shorter than body; segment I longest. Eyes feebly concave within. Front legs stout, slightly curved, the tibiae longer than femora, basal segment tarsi only half the length of apical one. Middle and hind legs long and slender, the femora extending far beyond the top of abdomen. Abdomen in wingless forms shorter than remainder of body, its side above flattened near base, obtusely carinate and inflexed towards the apex. In winged forms pronotum subquadrate, fused with mesonotum, narrowly rounded behind; wings narrowed posteriorly and surpassing abdomen.

Only one species is known from Northeastern United States.

1. *Limnogonus hesione* (Kirkaldy, 1902)

Fig. 15

Black, thickly clothed above with minute oppressed pubescence, beneath with silvery pubescence; transverse spot on base of head, margin of hind prolongation of pronotum, and spot on anterior portion of pronotum reddish-yellow. Segment I of antennae slightly less than II and III united; segments II, III and IV of about equal length. Wingless forms oblong-oval, rather robust; pronotum short, slightly produced posteriorly in male, more strongly so in female to cover front portion of mesonotum, mesonotum large. Both winged and wingless forms known.

Length, 4.5-8 mm.; width 1.4-1.8 mm.

This species is found along the edges of lakes and ponds, usually in large schools.

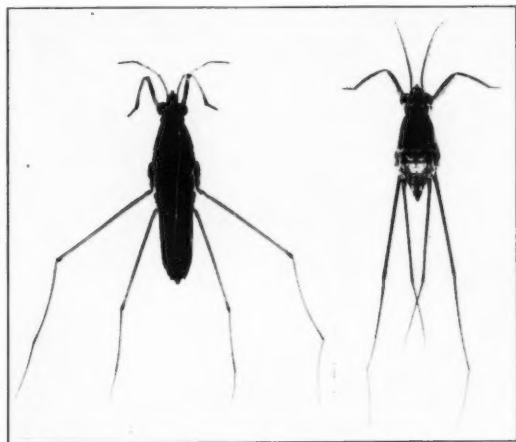


Fig. 14. *Gerris marginalis*, male, actual length 10 mm. (15) *Limnogonus hesione*, male, actual length 6 mm.

14

15

In Indiana it has been collected in only two counties: Kosciusko by Blatchley and Gould, and in Carroll by the authors. Winged forms are uncommon.

## Subfamily HALOBATINAE Bianchi, 1896

The members of this family are small insects with short, broad bodies. They are black in color often marked with yellow. The eyes are convexly rounded on the inner margins and not emarginate. The abdomen is usually very short. Both winged and wingless forms are known.

This subfamily is represented in Indiana by three genera, six species and one variety.



## Key to the genera of Indiana Halcbatinae

1. Antennal segment I subequal in length to other three united, distinctly longer than II and III ----- *Metrobates*.
- 1'. Antennal segment I much shorter than other three united, sometimes shorter than II and III ----- 2.
2. Abdomen as long as remainder of body, pointed at apex. Antennal segment IV subequal to III in length ----- *Rheumatobates*.
- 2'. Abdomen much shorter than remainder of body. Antennal segment IV distinctly longer than III ----- *Trepobates*.

## I. Genus METROBATES Uhler, 1871

Body short and robust. Wingless forms with head broader across eyes than long, much narrower than mesonotum, pronotum wider than long, concave at middle, not fused with mesonotum; mesonotum very large, with a wide shallow, median impression. Eyes very large; inner margin convexly rounded. Front legs short, segment I of tarsi about one-fourth the length of II; middle and hind legs slender, very long. Winged forms rare. Hind lobe of pronotum extending back in form of broad triangle; wings longer than abdomen.

Only one species is known from Northeastern United States.

1. *Metrobates hesperius* Uhler, 1871

Fig. 18

Black, covered with velvety pubescence and with a dull leaden bloom. Spots on base of antennal segment I, on head and on pronotum dull yellow; antennae and legs dark brown, coxae yellow. Antennae almost equal in length to body; segment I thickened at base, slightly curved and as long as others united. Hind tarsi one-segmented; front tarsi with claws placed one-third in front of tip.

Length, 3.5 mm.; width 1.3-1.8 mm.

This species occurs upon the surface of slow-moving streams and lakes, usually in large numbers. Sometimes they congregate in a large, black colony in the quiet eddies below a huge boulder in rapid-flowing streams.

Specimens in the Purdue Collection are from the following counties: Allen, Bartholomew, Cass, Carroll, Dubois, Franklin, Fulton, Grant, Harrison, Johnson, Kosciusko, Lawrence, Monroe, Noble, Parke, Putnam, Rush, Tippecanoe and Whitley. The dates of collection are from July 11 to October 17.

## II. Genus RHEUMATOBATES Bergroth, 1892

Small, oblong forms, having a square head, large eyes. The antennae of males curiously curved and armed with several short, acute spines. In wingless forms pronotum much wider than long; mesonotum somewhat square, three or more times longer than pronotum. In the rare winged individuals wings much longer than abdomen, with pronotum covering mesonotum. Front legs stout, short, tibiae less than half the length of femur, basal segment of tarsi small, the second segment with apical half flattened beneath and claws

inserted near the middle. Middle and hind legs long and slender. Antennal segment I scarcely, if any longer than II and III united; segment IV equal to or shorter than III. Abdomen as long as remainder of body, strongly tapering toward the apex. Two species and a variety are known from North-eastern United States with only the variety recorded from Indiana by Blatchley (1926).

1. *Rheumatobates rileyi* Bergroth, 1892

Black, oblong striders with undersurface dusky yellow. Transverse median spot on pronotum, a diamond-shaped median spot on mesonotum, a round spot above middle coxae, the front femora and the reflexed connexiva usually yellow. Male with segment I of antennae thickened apically, armed beneath at apical third with one or two short spines; segment II very short, armed with slender spine near base; III strongly curved, with shallow spiny depression at apical third; IV with apical portion curved, acute, armed beyond the middle with a strong tooth. Male with middle femora fringed with long, straight hairs, middle tibiae with hooked hairs on inner side of basal half; hind femora somewhat swollen, curved to form a circle when held behind body; fringed on basal third with a row of long hairs and two tufts of hairs at apex; hind tibiae narrowed and curved slightly outward at the basal third with a tuft of long hairs glued together, projecting backward from this curved portion. Antennae and legs of female unmodified.

Length, 2.8-3 mm.; width 0.8 mm.

Specimens in the Purdue Collection are from Decatur and Ripley counties, collected on October 15 by G. E. Gould.

1a. *Rheumatobates rileyi* var. *palosi* Blatchley, 1926

Figs. 2, 16.

This variety resembles the species, differing from it primarily in the location of the "strong tooth" on the fourth antennal segment. This "tooth" arises before the middle of the segment in the variety instead of beyond the middle as in the species. The hind tibiae are more slender and straight, and the hairs of the hind femora are more numerous in the variety. The females of the two forms are very difficult to separate. The color markings in both the species and the variety are variable and are not good diagnostic characters.

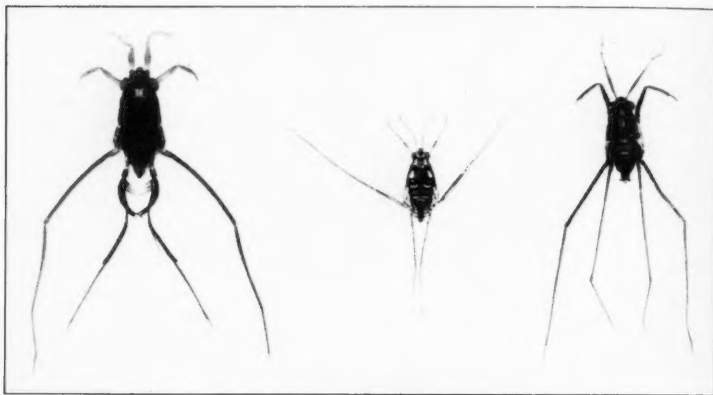
Length, 2.7-2.9 mm.; width 0.8 mm.

The varietal form is common throughout the middle west. These curious little insects are found in quiet waters of ponds or backwater of running streams, often in company with *Trepobates*.

Specimens in the Purdue Collection were taken in the following counties: Allen, Carroll, Clay, Franklin, Hamilton, Huntington, Jennings, Kosciusko, Lake, Tippecanoe, Vermillion, Wabash and Whitley between the dates of June 19 and October 17. Blatchley described this variety from Marion County.

## III. Genus TREPOBATES Uhler, 1894

Short, robust insects with short head, sloping in front, the space between the eyes equal to length of eye. Antennal segment I longest, II shortest, IV a little longer than III. Pronotum of wingless form truncate at front and



16

17

18

Fig. 16. *Rheumatobates rileyi* var. *palosi*, male, actual length 2.8 mm. (17) *Trepobates inermis*, female, actual length 3.5 mm. (18) *Metrobates hesperius*, male, actual length 3.5 mm.

hind margins, wider than longer; mesonotum square, twice as long as pronotum, truncate behind; metanotum in part showing. Abdomen short and conical; the connexiva strongly reflexed. Front legs short; middle and hind legs long; front tarsi with two segments, hind with one. In winged forms pronotum covers meso- and metanotum; wings extending much beyond the abdomen, with the basal portion blackish and membrane dark brown, truncate at base (dealating sutures of Drake and Harris) where it is often broken off.

Four species have been described from Northeastern United States, but there is some confusion as to their true identity. Two species, *pictus* (H.S.) and *inermis* Esaki, are readily recognized from our material, while a third, *subnuditus*, was described in 1926 by Esaki from Indiana. Certain male specimens from Southern Indiana seem to fit the description of the fourth species, *knighti* Drake & Harris, known from Missouri, Arkansas and Kansas. Members of this genus are found on the backwater pools of streams and near the shore of ponds.

## Key to the Indiana Species of Trepobates

- |     |         |       |    |
|-----|---------|-------|----|
| 1.  | Males   | ----- | 2. |
| 1'. | Females | ----- | 5. |

- 2 (1). Fringe of hairs on inside of femora and base of tibiae of middle legs as long as diameter of leg at point of origin ----- 3.
- 2' (1). Fringe of hairs on inside of femora and base of tibiae of middle legs not over half as long as diameter of leg at point of origin ----- *T. pictus*.
- 3 (2). A row of long hairs on inner side of antennal segment III, often closely pressed to the segment. First genital segment rather thickly clothed beneath with moderately long, erect, pale hairs ----- *T. knighti*.
- 3' (2). Antennal segment III without long hairs. The first genital segment not noticeably hairy beneath ----- 4.
- 4 (3'). Antennal segment II distinctly shorter than III. Under surface of second genital segment thickly beset with hairs ----- *T. inermis*.
- 4' (3'). Antennal segments II and III subequal. Under surface of second genital segment without long hairs ----- *T. subnitidus*.
- 5 (1'). Connexiva (lateral margin of abdomen) extended upward at posterior ends into long spine-like processes ----- *T. knighti*.
- 5' (1'). Posterior ends of connexiva not extended into long spine-like processes ----- 6.
- 6 (5'). Posterior margin of last ventral segment of abdomen clothed with long hairs. In wingless forms the posterior margin of mesonotum prolonged backward into a horn-like process ----- *T. pictus*.
- 6' (5'). Posterior margin of last ventral segment of abdomen without long hairs. Mesonotum not prolonged backward into a horn-like process ----- 7.
- 7 (6.). Antennal segments II and III subequal in length ----- *T. subnitidus*.
- 7' (6'). Antennal segment II distinctly shorter than III ----- *T. inermis*.

#### 1. *Trepobates pictus* (Herrich-Schaeffer, 1848)

Apterous forms: Color pattern variable, yellow with black markings usually predominant. Pronotum twice as wide as long. Intermediate femora and tibiae of male clothed on inner margin with short hairs never longer than half the diameter of the appendage to which it is attached; last segment of venter at middle only twice as long as the preceding; genital segments without long hairs. Mesonotum of female produced backward into a hairy, horn-like process; edge of connexival hairs, their apices produced slightly posteriorly; hind femora without longer hairs on basal portion.

Winged forms: General color dark brown above. Pronotum prolonged posteriorly, the hind margin broadly triangular. Wings surpassing abdomen by half their length.

Length, 3-4 mm.; width 1.3-1.8 mm.

Formerly several species were reported under this name. The females are readily recognized by the mesonotal horn. Blatchley (1926) no doubt had specimens of this species.

In the Purdue Collection only three counties, Clay, Harrison, and Tippecanoe, are represented.

#### 2. *Trepobates inermis* Esaki, 1926

Fig. 17

Apterous forms: Color pattern variable, usually black with yellow markings. Posterior margin of mesonotum truncate. Basal portion of tibiae and femora of middle legs in male clothed with hairs equal in length to diameter

of the appendage where it is attached; last genital segment hairy beneath. Posterior margin of last ventral segment of abdomen in female without long hairs; edges of connexiva hairy; base of abdomen with patch of long hairs.

Winged forms: General color brownish-black above. Pronotum produced posteriorly; the hind margin broadly triangular; the marginal flavous (dull yellow) stripe always present on posterior margins and often running forward on both sides to extend across head, in which case a small median spot is found on base of pronotum. Wings extend half their length beyond abdomen.

Length, 3.2-4 mm., with wings often 5 mm.; width 1.3-1.8 mm.

This species is common throughout Indiana, having been collected in the following counties: Allen, Bartholomew, Carroll, Clay, Decatur, Dubois, Franklin, Grant, Harrison, Huntington, Jennings, Johnson, Kosciusko, Lawrence, Marion, Monroe, Owen, Parke, Putnam, Ripley, Rush, Tippecanoe, Wabash, Wells and Whitley.

### 3. *Trepobates subnitidus* Esaki, 1926

This species was described from specimens collected in Lake County, Indiana. There is some doubt about the identity of this form. Drake and Harris (1932) state that much of their material seems similar to *inermis* and that the genitalia of a long series of specimens must be studied to determine if this form is a distinct species. Distinguishing characters are antennal segment III without long hairs; segments III and II about equal in length; first genital segment not noticeably hairy beneath and the second segment without long hairs beneath.

Length, 3.5 mm.; width 1.8 mm.

### 4. *Trepobates knighti* Drake & Harris, 1928

Apterous forms: Pronotum more than half as long as wide; anterior femora strongly bowed. Color blackish with yellow or fuscous markings. Antennal length variable. Antennal segment III of male with a row of fine, long hairs along lower front margin extending forward, sometimes stuck to segment. Intermediate femora and bases of tibiae densely clothed with hairs equal to or longer than the diameter of the segment to which they are attached; first genital segment clothed with thick, short hair beneath. Last segment of venter in female not hairy; connexiva produced outward and upward into long, spine-like processes.

Length, 3.00-4.3 mm.; width 1.4-1.6 mm.

Males from certain counties in Southern Indiana agree with the description, although no female with the distinctive connexival spines has been found. Previously this species has been recorded from Missouri, Arkansas, Oklahoma and Iowa. There are specimens in the Purdue Collection from Arkansas, Missouri and Kansas.

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# Contributions to the Herpetology of Texas

## I. Frogs of the Genus *Pseudacris* \*

Charles E. Burt

### Introduction

This is the first of a series of contributions to the knowledge of the amphibians and reptiles of Texas. Beginning with the academic year of 1930-1931, when I was Professor of Biology at Trinity University (Waxahachie), data have been consistently gathered. Many collecting and observational tours have been made over the state, partly with the aid of grants advanced by Dr. Alexander Wetmore, Director of the United States National Museum, from the funds of the Smithsonian Institution. In addition, the extensive herpetological collection of the United States National Museum has been examined, through the permission of Dr. Leonhard Stejneger and with the assistance of Dr. Doris M. Cochran. I am also grateful to Mr. William J. Tucker, Executive Secretary of the Texas State Game, Fish, and Oyster Commission for permission (obtained through Dr. Wetmore) to seine and otherwise to collect aquatic life in the State in the interests of the United States National Museum. In the early part of the project specimens were widely disseminated, but the bulk of the collection is in the United States National Museum.

The following comments deal with four species of false (or swamp) tree frogs of the genus *Pseudacris*. Judging from the available literature, it seems that one of these forms (*P. ocularis*) has not been taken perviously in Texas or in any place so far to the west.

### Key

1. Body length of adults usually less than 30 mm.; dark markings on back finer, irregular, broken, or largely eliminated, also less diagonal and often with a definite longitudinal arrangement .....2  
Body length of adults often more than 30 mm.; dark markings on back usually coarser and very diagonal, but sometimes obsolete on large specimens. ....*P. streckeri* Wright and Wright.
2. Body length of adults over 19 mm.; body stouter, elongately ovoid as viewed from above .....3.  
Body length of adults less than 19 mm.; body slender, elongate, delicate; dorsal and lateral darak markings often relatively obscure posteriorly. ....*P. ocularis* (Holbrook).
3. A continuous vertebral dark stripe usually present for a considerable distance; back with a predominance of dark stripes. ....*P. nigrata triseriata* (Wied).  
Vertebral region usually either spotted or predominantly light in color; back with a predominance of dark spots. ....*P. nigrata clarkii* (Baird).

\* Contribution from the Biological Laboratory of Southwestern College.



*Pseudacris ocularis* (Holbrook)

Two of these little frogs resemble examples taken in Brantley County, Georgia, in 1933. They were secured one mile south of Mount Enterprise, Rusk County, on June 17, 1934, at the border of a small wooded stream. The moist woods were undergrown with grass and much scattered drift was in evidence. Here *ocularis* was found leaping about on the shaded forest floor, where it was associated with such forms as American "chameleons," spiny lizards, cricket frogs, black lubber grasshoppers, and black winged damsel flies.

*Pseudacris streckeri* Wright and Wright

The frogs listed below were collected in the section of Texas from which *P. occidentalis* and *P. ornata* have been occasionally reported, notably by Cope and Strecker. The large number of specimens that I have recently collected agree in the possession of the following diagnostic characters; body stout, 31-40 mm. long in adults; width of head at tympanum entering body length 2.58 to 3.16 times; muzzle rounded in profile, projecting; nostril placed approximately half way between muzzle and orbit; hind foot distinctly webbed, with subarticular tubercles; heel of adults not reaching beyond tympanum when applied forward; skin of upper surfaces smooth.

The variations of the *Pseudacris* frogs appear to be so uniformly graded that I am forced to regard the series as belonging to only one species, just as Strecker (1915, p. 48) was inclined to do, and as Wright and Wright have done recently (1933, p. 102). It appears that Cope (1889) confused his *ornata* and his *occidentalis*, both as to diagnostic characters and as to range, and that workers prior to 1923 have done little to untangle this complication. Historically, we find that *ornata* was described by Holbrook in 1838 from near Charleston, South Carolina, while *occidentalis* was diagnosed by Baird and Girard in 1853 in a paper dealing only with western and middle-western species. There is apparently no reason to doubt that the type locality given for *occidentalis* (San Francisco) was an error, or to consider *occidentalis* as anything but a synonym of *Hyla regilla*. Slevin (1928, p. 114) listed this conclusion in his synonymy. The present *streckeri* is of definitely middle-western origin (as compared with *ornata* of eastern areas) and in theory it would appear logical to accept *streckeri* as the name for the Texas form in case it is specifically or subspecifically distinct from the eastern *ornata*. To date I have made no critical comparison with eastern specimens, so there is nothing to offer in this regard. Mr. Karl P. Schmidt has found what he believes to be *ornata* in Louisiana.

An examination of the key to these frogs presented by Cope (1889, p. 332) indicates that he probably used Texas specimens as a partial basis of his conception of *ornata*. However, it is interesting to note that Cope, who may have used very few specimens in the preparation of his diagnoses, found the width of the head of *ornata* at the tympanum to enter the body length 2.50 to 2.66 times, and of *occidentalis*, 3.00 to 3.50 times. In the present

instance the range is between 2.58 and 3.16 times, which is an intermediate gradation tending to connect the two extremes, but coming closer to Cope's *occidentalis* than to his *ornata*.

In the character of the skin of the upper surfaces *P. streckeri* differs from *P. nigrita clarkii* in the same way that the dorsal integument of *Hyla versicolor chrysoscelis* differs from that of typical *H. versicolor versicolor*. Also, the color patterns and general size of *Hyla versicolor chrysoscelis* and *Pseudacris streckeri* are suggestive of each other to a rather marked extent. However, the two frogs may be distinguished at once in the field by their voices and in the laboratory the *Hyla* shows expanded digital pads while the *Pseudacris* shows remarkably reduced ones.

*Streckeri* has a vocal sac that is greenish yellow when expanded (being darker anteriorly, but lighter posteriorly and at the edges). The loins and posterior surfaces of the hind legs usually show a yellowish-green coloration similar to that of the vocal sac, while the under surfaces of the extremities are pink or purple. The ventral surface of the body is whitish, without dark markings. Apparently there is always a dark stripe of varying width which extends from the tip of the snout through the nostril to the eye on each side, and the tympanum is usually crossed by a posterior prolongation of this streak, which frequently ends at the shoulder but may extend backward as far as the groin. The upper lip usually shows a dark cheek patch at the antero-ventral border of the orbit, which separates a white labial patch into two spots, the anterior light spot lying somewhat ventrally to the nostril and the posterior one in front of the tympanum. The dorsal and lateral color pattern of the trunk varies remarkably. The back and sides display darker markings placed upon a gray to grayish brown ground color, although certain individuals have patches of bright green on their backs. The dark markings, which may be either deep brown or black, are usually more intense laterally, although certain individuals have only rudiments of them on the sides; and dorsally dark markings are usually faint, being so obscure at times that superficially the back approaches a unicolor condition. In a few examples these dark elements tend to form longitudinal lateral stripes which suggest the pattern of the eastern *Pseudacris nigrita triseriata*, but usually they are broken or altered into irregular (or oblique) patches or bars which may convey no suggestion of the longitudinal in their arrangement. The skin of *streckeri* is granular ventrally and smooth or very slightly granular dorsally, large tubercles or warts being absent.

During the vocal season individuals of this species, congregate in the vicinity of both running and still bodies of water. The greatest number was noted at the margins of moderate-sized ponds that had risen and expanded over grassy areas, thus providing grass stems for the frogs to cling to after they had undergone migration to the water.

In 1930 and 1931 *Pseudacris streckeri* was collected at night after its song had revealed its position, although it often sings in the daytime. The song, which may carry well over a mile and often sounds nearer than it is,

was commonly heard in Ellis County from December 15 until April 10, although specimens were collected only between February 16 and April 4. The call is a rhythmic series of sharp piping notes, suggesting the eastern *Hyla crucifera*. The singing progresses in cycles, periods of song being followed by intervals of silence. While collecting was taking place, captive individuals could often be induced to sing by vibrating the wet collecting bag (cloth), and this would sometimes initiate a chorus of the free frogs in the neighborhood. In specific instances full song was often preceded by short hoarse chirps of varying degrees of loudness. As in the case of *Pseudacris nigrita clarkii*, singing frogs of this species are extremely cautious and hard to approach in the day time or on bright moonlight nights, due to a cessation of song upon the slightest disturbance. However, on the darker nights many individuals continued to sing even when exposed by a strong beam of light and these were easily approached and collected, each frog being clumsy in its attempt to escape, if such activity were undertaken at all. In general, also, there was usually more song on warmer winter nights than on the colder ones. Thus on the relatively mild evening of February 21 twenty specimens were taken, whereas on the windy, drizzly, and relatively cold evening of February 27 only six specimens were obtained. As a matter of checking, subsequent collecting at the second habitat on the relatively warm evening of March 5 netted 37 specimens, indicating that the ecological differentiation cited above was not fortuitous.

Only a few facts pertaining to the life history of *streckeri* were observed in 1931. On February 17 captive males displayed the clasping instinct at numerous times in the laboratory, although clasping pairs were not found in the field at this date. On February 21 specimens were out in large numbers in Ellis County, with males attracting females, but no clasping pairs or egg masses were located. The females were much more shy and harder to catch than the males, diving downward and attempting to hide in bottom debris when exposed by a flash of light. Likewise, on March 5, *streckeri* was abundant and in full song in Dallas County, where several clasping couples were observed and collected. In 1934 two pairs were found in amplexus on March 16 as they clung to grass stems at the edge of a small stream in Hood County. On the following day a number of individuals were found in Erath County under rocks on a sloping hillside above a temporary pond. Burrows seen in several instances suggested that some of the frogs may have hibernated in the earth during the winter. At still another point in Erath County a specimen was secured in rotted wood under a log near a small stream.

Some county records of *P. streckeri* may be listed as follows:

BELL: 3 mi. S. Belton and 3 mi. S. W. Salado (Apr. 1, 1931). BEXAR: Helotes (G. W. Marnock, Nov. 30, 1883). BRAZOS: College Station (G. W. Goldsmith). BROOKS: 2 mi. S. Encino (Apr. 4, 1931). COOKE: Gainesville (G. H. Ragsdale). DALLAS: 4 mi. S. Dallas (Mar. 5, 1931). ELLIS: 1 mi. W. Waxahachie (Feb. 16, 1931), 6 mi. S. E. Midlothian (Mar. 19, 1931). ERATH: 3 mi. N. E. Dublin (Mar. 17, 1934). HAYS: Dripping Springs (Mar. 6, 1931). HOOD: 2 mi. S. Granbury (Mar. 16, 1934). KENDALL: (R. T. Young, Mar. 28, 1900). McCULLOCH: Bady (Otis Sanders, 1932). McLENNAN: Waco (Huter Coll., Apr. 13, 1910). PARKER:

5 mi. N. E. Cresson (Mar. 16, 1931). TRAVIS: 14 mi. W. Cedar Valley (Mar. 6, 1931). WILLIAMSON: 1 mi. S. Jarrell (Apr. 1, 1931).

*Pseudacris nigrita clarkii* (Baird)

In 1931 (p. 12) I followed a suggestion of Mr. Karl P. Schmidt that the frog of the *nigrita* complex from central Texas (*clarkii*) should be recognized as distinct from more striped northern and eastern individuals (*triseriata*). The exact distribution of the two variants is not known. Intergradation occurs in southern Kansas (as in the area about Winfield, Cowley County) and perhaps in eastern Texas as well.

The vocal sac of *clarkii* is dark brown in contrast to the true cricket frog of similar size (*Acris gryllus*), whose throat is usually immaculate.

All adult specimens of *clarkii* taken between October 15, 1930, and May 22, 1931, were collected at night after their positions were revealed by song. The frogs sang at rainy periods all during the winter season. The characteristic habitat consists of the placid waters of relatively temporary roadside and meadow pools or ponds, which usually have risen in the winter so that a fringe of grass land is included in the area that they cover. Here the "prairie tree frogs" cling to grass or weed stems as they sing. Examples are secured not only in the more desolate lands, but also in cultivated fields (often near to human dwellings) and in barnyards. Individuals of this species are much harder to capture than are the toads and most of the common frogs (with the exception of *Gastrophryne*), for upon slight disturbances they release their holds on supporting vegetation and dive beneath the water where they are well concealed if the pool is not clear and shallow. *P. nigrita clarkii* frequently sings from the same pools as other amphibians and I have found singing adults to be associated at various times with such forms as *Bufo woodhousii*, *B. valliceps*, *Rana pipiens*, *Pseudacris streckeri*, *Acris gryllus*, and *Gastrophryne olivacea*. An adult *clarkii* was located under a rock on a hillside above a pond in Erath County on March 17, 1934. Several small hollowed out earthen tunnels were visible here as places where the frog may have undergone at least temporary hibernation.

By use of a dip net, tadpoles and metamorphosing young of *Pseudacris triseriata clarkii* were obtained in Comal County on April 2, 1931, from a pool that was covered by a thick scum of algae. Here these forms were associated with the adults of *Acris gryllus* and the larvae of *Rana pipiens* and *Ambystoma texanum*. Numerous metamorphosing young, both tailed and tailless, were gathered above the edge of a small pond in Wise County on the chilly morning of April 17. Some were under stones and some in the grass. All were semi-dormant, usually making no attempt to escape when approached. The transforming larvae of *clarkii* develops the minute warts on the back that are so characteristic of adults, although the early tadpole does not have these markings.

Some county reports of the occurrence of *clarkii* follow:

BASTROP: 5 mi. N. W. McDade (June 5, 1935). BRAZORIA: Freeport (Ottys Sanders, March 10, 1936). BROWN: Brownwood (Sept. 4, 1935). COLEMAN: 2 mi. W. Santa Anna (Sept. 4, 1935). COMAL: 3 mi. S. W. New Braunfels (Apr. 2, 1931). COOKE: Gainesville (Ragsdale). DALLAS: 4 mi. S. Dallas (Oct. 18, 1931). ELLIS: Boyce and 4 mi. W. Ennis (Mar. 18, 1931), 4 mi. S. E. Midlothian (Feb. 23, 1931), and 5 mi. N. W. Waxachachie (Oct. 15, 1931). ERATH: 3 mi. N. E. Dublin (Mar. 17, 1934). GALVESTON: Galveston (M. Dean). GARZA: 14 mi. E. Post (Sanders, Mar. 29, 1934). HUNT: 2 mi. S. W. Greenville (Apr. 2, 1931). ROBERTSON: 4 mi. S. W. Hearne (June 4, 1935). SOMERVELL: 8 mi. N. E. Nemo (June 12, 1935). VICTORIA: Victoria (J. D. Mitchell, Dec. 11, 1904). WILLIAMSON: 1 mi. S. Jarrell (Apr. 1, 1931). WISE: 6 mi. S. E. Decatur (Apr. 17, 1931).

The type specimen (U. S. N. M. no. 3313) is from Galveston. The other specimens listed above are like it in all essential details.

*Pseudacris nigrita triseriata* (Wied)

Mr. Ottys Sanders took this little striped frog on highway No. 80 between Longview and Marshall in Harrison County, on March 31, 1934; and near Athens, Henderson County, on March 7, 1936, so *triseriata* is a denizen of eastern Texas.

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## An Insular Population of *Peromyscus maniculatus* subsp. with Mixed Racial Characters

William L. Engels

Among some mammals collected by Mr. R. A. Cumming in British Columbia and placed by him in the Museum of Vertebrate Zoology of the University of California there is a series of *Peromyscus maniculatus* from Bowen Island (16 specimens, of which 13 are adult) which presents an interesting, though puzzling, taxonomic problem. The adult specimens may be distinguished from representatives of any one of three neighboring named populations of *maniculatus*, yet the series shows no characters peculiar to it—it is different only in offering a unique combination of the distinguishing characters of the neighboring races.

Bowen Island is a small island about 12 miles northwest of Vancouver, lying in the mouth of Howe Sound, close to the mainland. This part of the British Columbian coast, as well as the Puget Sound region of Washington, is inhabited by white-footed mice belonging to the race *Peromyscus maniculatus austerus*. Between Bowen Island and Vancouver Island, on which occurs *Peromyscus maniculatus angustus*, lies the Strait of Georgia, here some 25 miles wide. Approximately 50 miles to the south of Bowen Island, on the west side of Haro Strait, lies Saturna Island, the type locality of *Peromyscus maniculatus saturatus*. Merely on the basis of geographical location, the Bowen Island population might be expected to resemble the mainland population (*austerus*), but it does so in color only.

*Austerus* is characterized by its size, which is medium, and by its very dark, sooty color. *Saturatus* is distinguished from it by being larger, with a larger, broader, more angular skull, by being somewhat lighter in color, with a conspicuous lateral line, and by having the tail shorter than the body. *Angustus* differs from *austerus* essentially only in color, being browner (less blackish).

The Bowen Island specimens are indistinguishable in color from those of the adjacent mainland (*austerus*), of which I have seen large series, in comparable pelage, from Hopkins Landing (Howe Sound), Vancouver and Seattle. They average much darker, more sooty above, than a series from Saturna Island (ten topotypes of *saturatus*) though there are a few intermediates in each series. The sides are darker (grayer), usually without a lateral line, and this line is indistinct in the few specimens showing it. The Saturna Island specimens are browner on the sides, with a distinct lateral line in most cases, and cinnamon in color. Vancouver Island specimens (*angustus*) are similar in color to those from Saturna Island, but lack the lateral line. Thus, there are two groups here, separable by color: the darker forms occur-

ring on the *east* side of the straits separating Vancouver Island and adjacent islands from the mainland, and lighter forms on the *west* side of these straits.

Skulls of the Bowen Island specimens are, however, larger than those from the mainland, with a little overlapping, and are broader and heavier. In this respect they are similar to skulls from Saturna Island, from which they can be distinguished, if at all, only with difficulty. Vancouver Island skulls are essentially like those from the mainland. Here then is a different geographical arrangement of characters: specimens with smaller skulls occurring on the mainland and on Vancouver Island; and specimens with larger skulls on the two small geographically intermediate islands.

About the same arrangement obtains with respect to the relative length of tail. In mainland specimens the tail exceeds, slightly, body length; in Vancouver Island specimens the tail about equals body length; and the Bowen Island specimens and the Saturna Island specimens both have tails shorter than the body.

These characters, and their geographical distribution, may be summarized briefly in the following scheme:

Tail shorter; skull larger:  
darker: Bowen Island  
lighter: Saturna Island

Tail longer; skull smaller:  
darker: mainland  
lighter: Vancouver Island

I am unable to find other characters which further distinguish these four populations in a satisfactory manner. The skull characters used by Hall (1932) to distinguish *angustus* of Vancouver Island from *austerus* of the mainland are not valid for series other than those he used. It would appear that there may be some slight average quantitative differences (*angustus* with longer nasals, shorter maxillary tooth-row) but these are so slight as to be negligible when based on any except very extensive series. The only possible perceptible qualitative difference is a very slight variation in the shape of the brain-case, which tends to be more rounded posteriorly in *angustus*.

It is equally difficult to separate the Saturna Island population from that of Bowen Island on skull characters, though the index *length of nasal: mastoid breadth* may provide a significant difference. The length of nasals exceeds the mastoid breadth in Saturna Island specimens, but the reverse is true of Bowen Island specimens. In three pairs of individuals, judged on the basis of tooth wear to be of equal age, this difference amounts, in each pair, to 10 per cent. Vancouver Island and mainland specimens also usually have the mastoid breadth exceeding the length of nasals, as in Bowen Island skulls. This possibly unique feature of the Saturna Island form does not effect any change in proportions of the skull outline, since the nasals are longer by reason of a greater elongation posteriorly.

There are slight average differences between the four populations with respect to the relative length of tail, which is, in the series examined by me, 53 per cent total length on the mainland, 50 per cent on Vancouver Island,



46 per cent on Bowen Island and 40 per cent on Saturna Island. On these one should not perhaps place much weight. Indeed, examination of the measurements of the Vancouver Island series mentioned by Hall (1932) shows the tail to average 49 per cent of total length (46.3-51.5) and for the mainland series, 51 per cent (48.2-53.1). The average of 10 topotypes of *saturatus* given by Bangs (cited in Osgood, 1909, p. 61) indicates the tail to be 42 per cent of total length. If these differences in percentage mean anything, they indicate that, as regards this character, mainland specimens overlap those of Vancouver Island, and these overlap those from Bowen Island. It would seem best to consider the populations as of two groups, one with tails about as long or longer than the body (Vancouver Island, mainland) and one with tails definitely shorter than the body (Bowen Island, Saturna Island), an assumption I had in mind when giving the scheme (above) summarizing the characters of the populations.

Thus these four populations differ essentially only in three characters, two of which go together (skull size and relative tail length; color). Theoretically, any two factors or factor groups afford four possible combinations. These four combinations are realized in the four populations in question. Is one justified, now, in recognizing, nomenclaturally, four races based on the four possible combinations of two groups of characters? In this case, I do not think so. Such recognition would result in four races with the same characters, differing merely in having these in four different combinations. Furthermore, the individual characters would have to be given different weights according to the combination in which they occurred; the two characters, *size of skull* and *relative length of tail*, would have no more weight than the single character, *color* (tone, not pattern).

The Bowen Island population, it would seem, ought rather to be looked upon as intermediate between *austerus* and *saturatus*. It has gone as far in differentiation from *austerus* as has *saturatus* with respect to size of skull, not quite as far with respect to relative length of tail; and as regards relative length of nasals as well as color it remains like *austerus*. It has no single unique character and it is distinguished by a mixture of the characters of *saturatus* and *austerus*. It could be defined clearly and definitely as: large-bodied, short-tailed *austerus*; or equally well as: dark *saturatus*; and in no other fashion. For practical purposes (as for cataloging) it might be called *saturatus*, which it resembles in size of skull and relative length of tail, but its true significance is that of a population morphologically intermediate, geographically isolated.

The question resolves itself: What is the significance of morphological intermediates? It must be recognized that, whatever their origin, intermediates are of two types—those which are also geographically intermediate (i.e. occurring in an area of intergradation along the contiguous borders of the ranges of two closely allied, neighboring stocks—thus intergrades and those which are not geographically intermediate (e.g., occurring well within the confines of a given range, far from the area of intergradation). The morphological inter-

mediacy of the intergrades would seem to depend to some extent on their geographical intermediacy, being due *a*) to either immediate or more or less remote hybridization, or *b*) to intermediate differentiation because of the fading out of the conditions favoring, on either side, directive differentiation. Morphological intermediates *not* geographically intermediate could not ordinarily be in the nature of hybrids; they are, rather, in the nature of intermediate differentiates, the frequency of their occurrence being an expression of the relative heterozygosity of the race with respect to the characters which distinguish it.

An insular population, effectively isolated, could not be considered to owe its intermediate character solely to its geographical position, surely not in any appreciable degree to hybridization. It is comparable, as a population, to those individuals, intermediate in nature, which occur within the normal range of a race; it differs from them in being geographically isolated. Morphological intermediacy in such an insular population is readily understood on the assumption that there is represented an isolated stock, containing in its hereditary make-up the potentialities of neighboring allied stocks, but differentiating less rapidly and manifesting (as yet) no unique potentialities. That the mammalian fauna of Bowen Island may be generally intermediate in character is indicated by five shrews also collected there by Mr. Cumming. Three of these are distinctly *Sorex vagrans vancouverensis* (type locality Vancouver Island), two are intermediate between *vancouverensis* and *vagrans* of the mainland, none is clearly *vagrans*.\*

If then the Bowen Island *Peromyscus maniculatus* be considered intermediate, how is the race *angustus* of Vancouver Island to be treated? It is distinguished from *austerus* only by a relatively slight difference in color, no greater than that found between typical *saturatus* and the Bowen Island intermediates. The small apparent difference between *angustus* and *austerus* with regard to relative length of tail is less than the difference between *saturatus* and the Bowen Island intermediates. The skull is at least as similar to *austerus* as Bowen Island skulls are to typical *saturatus*, and perhaps more so.

It may be deemed inconsistent to disregard, on the one hand, a difference in color between Saturna Island and Bowen Island and to emphasize it, on the other, between Vancouver Island and the mainland. But the two cases are not entirely comparable. *Angustus* does not exactly resemble *saturatus* in color, as the Bowen Island population does resemble typical *austerus*. The ground color, especially on the sides, is a shade different and there is no distinct lateral line such as is so typical of *saturatus*. The Vancouver Island population then is not intermediate in the sense that the Bowen Island population is. If its slightly smaller tail shows an approach to the shorter-tailed forms, still it might be considered as developing in another direction as re-

\* Since this was written, E. Raymond Hall has shown the meadow-mice population of Bowen Island to be subspecifically distinct from that of Vancouver Island as well as from that of the mainland and has named it *Microtus townsendii cumming* (The Murrelet 17:15-16).

gards color. Examination of mainland and Vancouver Island series which were of nearly exactly comparable age and pelage, and which were large enough to show whether the apparent quantitative differences in the skull be real, would throw light on the question of the status of the race *angustus*; unfortunately, such series are not now available.

However, decisions on the claim of a given population to nomenclatural recognition are largely personal and arbitrary, and the making of such decisions is not an end in itself. I would emphasize, therefore, that the significance of these four populations lies in the peculiar geographical distribution of their common characters, without regard to purely nomenclatorial questions.

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## A Recent Grizzly Bear Skull Found Fossil in Oklahoma

J. Willis Stovall

*Ursus horribilis nelsoni* (Merriam).

*Ursus horribilis* Ord, Guthrie's Geography 2d. Amer. Ed. pp. 291, 300, 1815.

*Ursus nelsoni* Merriam, Proc. Biol. Soc. Washington xxvii pp. 190-191, Aug. 13, 1914.

The Skull described below was submitted to the writer by Mr. Truman Pearson, county supervisor of a mineral survey of the state of Oklahoma which is being conducted by the Oklahoma State Geological Survey as a Federal Aid Project. The skull is complete except that it contains only seven teeth, namely four molars and three premolars. The bone is unaltered and appears quite like recent bone.

The skull was discovered and collected by Mr. James Blaine in the N. W.  $\frac{1}{4}$  of the N. E.  $\frac{1}{4}$  of Sec. 11, T. 18 N., R. 18 W., near Lenora, Dewey County, Oklahoma. Discovery was made in a small canyon which cuts a bed of blue clay eight feet thick and which rests unconformably on the Permian Red Beds. Mr. Blaine has kindly loaned the skull to the University for an indefinite period of time.



Fig. 1. *Ursus horribilis nelsoni*, (Merriam). Left side of the skull.  
About  $\frac{1}{4}$  natural size.

Interest was aroused by the similarity of this skull to two grizzly bear skulls of unquestioned Pleistocene age previously found in western Oklahoma and described by the writer and C. Stuart Johnston.<sup>1</sup> It differs from these two skulls in that it is much smaller and it differs also in other minor details. It has the pronounced frontal shield and a strong sagittal crest of other similar bears. In spite of the proximity of the range and its general resemblance to the two latter species its affinities appear to lie closer to *Ursus nelsoni* than to *U. texensis texensis* or *U. texensis navaho*.

<sup>1</sup> Stovall, J. Willis and Johnston, C. Stuart. Two Fossil Grizzly Bears from the Pleistocene of Oklahoma; The Journal of Geology, February-March, 1935.

The muzzle is more pointed than the average *U. horribilis*. The posterior half of the frontal shield is flat and terminates in a point 85 mm. back of the orbits and at about the fronto-parietal suture. This is probably a female character. The anterior half of the frontal shield is slightly convex and contains a shallow sulcus about 25 mm. long. The sagittal crest is straight and 100 mm. in length. The lambdoidal crest projects out over the occipital condyles. The external auditory meatus is recurved and upturned. The mastoids are strong and slightly inclined forward. The postorbital processes are peglike and slightly hooked posteriorly. The postpalatal shelf is broad and depressed in the posterior region, and is 55 mm. in width at the posterior end of the last molars. The postpalatal notch is short and constricted posteriorly, giving it a somewhat ovate form. The palate is broad and deeply excavate and has pronounced arterial depressions. The basal length of the skull is 266 mm., the interorbital breadth is 70 mm., the palatal length is 140 mm. The lacrimal foramen is inside the orbit. The facial index is .50. The cranial is .63.



Fig. 2. *Ursus horribilis nelsoni*, (Merriam). Palatal view of the skull showing well worn molars and great zygomatic breadth. About  $\frac{1}{4}$  natural size.

The molars are badly worn and all sutures are thoroughly ankylosed, indicative of old age. The alveoli of the canines indicate teeth of small or medium size. The first molar is 17 mm. in length and 13 mm. in width. The second molar is 25 mm. in length and 15 mm. in width.

*Comparisons.*—The pronounced frontal shield and high sagittal crest establish the grizzly affinities of this specimen. Merriam<sup>2</sup> indicates extremes of 260 mm. (An average of three adult female *U. nelsoni*) and 380 mm. (*U. gyas*) for the basal length in the measurements taken in his reviews of the grizzly bears. The basal length of this skull exceeds that of *U. nelsoni* by only 6 mm. The skull of *nelsoni* is described as "small and wolflike." However, its cranial index is .64, while it is .63 in this specimen which is certainly

<sup>2</sup> Merriam, C. Hart. Review of the Grizzly and Big Brown Bears of North America; Bulletin No. 41, U. S. Dept. of Agriculture, 1918.

not wolflike. The wolves have a cranial index of .45 (plus or minus). The skull is, therefore, much longer than it is wide. The relative length of the facial region of the wolf skull is much greater than in the bears. Both of these bear skulls have a shallow sulcus in the frontal shield, in this specimen it lies in the anterior part. The palate is 140 mm. contrasted with 149 mm. in *nelsoni* (an adult male) and 138 mm. average for three adult females. The interorbital breadth is 70 mm. against 65 mm. in an old male. In both specimens the postorbital process is peglike, but in this individual it is hooked posteriorly. The teeth are small in both specimens. The zygomatic breadth is 169 mm. against 168 in *U. nelsoni*.

*U. texensis texensis* is a much larger individual, having a basal length of 308 mm., and a zygomatic breadth of 218 mm. The interorbital breadth is, however, 70 mm. in this individual and only 71 mm. in the large *texensis*. Both have a frontal shield which is "slightly depressed medially" and "pointed posteriorly." In each the rostrum is narrow; the palate is broad and deeply excavated between the molars.

*U. texensis navaho* also appears to be a somewhat larger bear having a palatal length of 157 mm. against 140 mm. and an interorbital breadth of 81 mm. against 70 mm.

It is thus possible that this bear could be a variant of either of the three described above. Indeed it is possible that it could be a variant of some as yet undescribed form. We feel certain, however, that it is a variety and not a distinct species, for it appears that Merriam<sup>3</sup> was no more justified in establishing his sixty-six species and varieties of grizzly and big brown bears than one would be in making a large number of species out of the common Virginia Deer, *Odocoileus virginianus*, or of Man, *Homo sapiens*. The latter species is probably more variable than the grizzly bears. The variants of the grizzly bears are probably best illustrated by the disparity of the cranial and facial indices in a group of skulls of the same species. Four Yukon grizzly bear skulls in the University of Oklahoma Museum have cranial indices as follows; .57, .58, .60, and .63. The facial indices of the same group, given in the same order, are as follows; .43, .45, .41, and .40. Such variations as these are found when the skulls in Merriam's paper were computed for their facial and cranial indices. (The cranial index is obtained by dividing the zygomatic breadth by the basal length and the facial index is found by dividing the interorbital breadth by the palatal length.) In view of the above relationships, it seems advisable to us to designate this skull provisionally as *Ursus horribilis nelsoni*. If this conclusion is correct, the range of this form is extended from Durango, Mexico, to Oklahoma, and perhaps farther.

<sup>3</sup> Op. Cit.

## Book Reviews

THE BOOK OF THE SEASHORE, by Howard J. Shannon. Garden City, Doubleday, Doran and Co., 1935. xxvii + 281 pp. \$3.50.

For more than a quarter century, Howard J. Shannon has studied the biology and physiography of the Long Island shore; this book embodies his results. It is neither technical nor avowedly popular. It is natural history of the sort that we generally associate with such names as White, the Peckhams and C. J. Herrick. Without adopting the format of a scientific contribution, it offers an abundance of data not to be found in technical volumes.

Most of these bear upon animal behavior, the subjects ranging from insects and crabs to mice and sandpipers. Of special interest are chapters on the Ethiops wasp, on *Psammochares atlanticus* (discovered by Mr. Shannon), and on the ghost crab. There also are excellent chapters on the responses of plants to the varied habitats of the shore. One chapter brings together the substance of the author's scattered papers on butterfly migration. On the geologic side, there is an excellent resumé of the development of Long Island and its sedimentary rocks, as well as an account of coast-line changes. Instead of footnotes, detailed and semi-technical comments are put into an appendix. There is an accurate list of plants and animals discussed, and an index.

Illustrations consist of Mr. Shannon's own drawings. Though not wholly acceptable as art, they possess clarity, detail and evident fidelity which make them acceptable as scientific records to a degree that photographs rarely attain. No camera could match the illustrations of ghost crab behavior facing page 188 or the drawing of a *Polydora* building its tube that faces page 76. Even the figures showing results of fifteen years' erosion of dunes (page 234) probably are superior to photographs. As I several times have told prospective contributors to this journal: even a good photograph may be less detailed, less truthful, than a drawing conscientiously, if somewhat inartistically, done.

The book's chief defects are two. The first is a title that does not suggest the detail with which it treats one region that lies within reach of many students. The second is a prolix, Victorian style that fails to match the freshness and accuracy of the author's data, or to make pleasant reading. —C. L. FENTON.

RELATIVE EFFICIENCY OF ROOTS OF PLANTS IN PROTECTING  
THE SOIL FROM EROSION, by Joseph Kramer and J. E. Weaver. Bulletin  
12, Conservation Department of the Conservation and Survey Division, University  
of Nebraska. Lincoln, Nebraska, 1936. 94 pp., 37 figs.

Careful analyses of soil types covered with plants were carried out by the use of ingenious methods to ascertain the "relative efficiency of roots and tops of plants in protecting the soil from erosion" and compared with like soils devoid of living plants. The studies embrace a great variety of plants, i.e. field, pasture, and garden crops as well as a number of weeds, buckbrush, and native grasses. The rates of erosion were determined and the great importance of plant cover in the protection of soil from erosion and in the maintenance of its fertility demonstrated. Undoubtedly a most opportune investigation of considerable theoretical and wide practical significance. —TH. JUST.



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